Inconspicuous, recovering, or northward shift: Status and management of the white shark (*Carcharodon carcharias*) in Atlantic Canada

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Abstract

Although white sharks (*Carcharodon carcharias*) have been considered rare in Atlantic Canada waters, recent sighting records indicate a potentially increasing presence. We combine historical to present sighting data with satellite telemetry tracks of large juvenile/adult white sharks tagged in U.S. (n = 9) and Atlantic Canada waters (n = 17) to show seasonal white shark presence and distribution in Atlantic Canada, returns by individuals over multiple years, and high site fidelity to the region. Telemetry data indicate that white sharks are a more common and consistent occurrence in Canadian waters than previously thought, presenting two potential scenarios: 1) tagging technology is revealing white shark presence that was historically cryptic, and/or 2) a northward range expansion of white sharks in the Northwest Atlantic, potentially due to climate change, population recovery, and/or increasing pinniped prey. Given combined sighting and telemetry data indicate a current need for proactive management of white sharks in Atlantic Canada waters, we propose the basis for a management action plan, addressing conservation priorities, management goals and research incentives while considering the potential for human-shark interactions.

Introduction

The distribution and abundance of species are rarely static, but fluctuate through time and space in response to the stochasticity of ecological and environmental conditions and anthropogenic influences (Brown et al. 1996). This is especially true in marine biomes, which are characterized by high habitat connectivity and limited barriers to species dispersal (Macpherson and Duarte 1994) and face increasing exploitation rates (Pauly and Zeller 2016).

Shifts in species distributions can be inherent life cycle components of an organism as ontogenetic changes in diet and space use (Werner and Gilliam 1984), or modified as a result of environmental changes, disturbances to trophic and community structure, and/or human exploitation (Dunne et al. 2002; Perry et al. 2005; García Molinos et al. 2016). For example, the overfishing and collapse of Atlantic cod (*Gadus morhua*) in the Northwest Atlantic ultimately led to the expansion of several prey species' ranges (Mason 2002). In addition, several species distributions have demonstrated marked shifts in response to climate change (Perry et al. 2005; García Molinos et al. 2016). Zooplankton in the North Atlantic and marine fish in the North Sea are shifting rapidly northward in response to rising sea surface temperatures (Beaugrand et al. 2009) with the speed and direction of regional climate shifts strongly influencing the direction and magnitude of species' shifts (Pinsky et al. 2013). However, the impact of these altered species distributions on overall ecosystem function is poorly understood. In order to effectively manage marine species' and ecosystems, management plans must account for the dynamic nature of our changing oceans and the potential for species' distribution shifts (Pecl et al. 2017).

The white shark (*Carcharodon carcharias*) is a long-lived, apex predator with globally distributed populations in temperate to tropical waters (Compagno et al. 1997; Huveneers et al. 2018). It is considered a highly mobile species that undertakes basin-scale migrations between near-shore coastal environments and pelagic waters (Bonfil et al. 2005; Jorgensen et al. 2010). The drivers of such mobility are diverse, including movements to aggregate in offshore waters potentially for feeding, mating and gestation (*e.g.*, off the Northeastern Pacific Shared Offshore Foraging Area or 'white shark café'; Domeier and Nasby-Lucas 2008; and the proposed Northwest Atlantic Shared Foraging Area or NASFA), moving into coastal environments to give birth (*e.g.*, Domeier and Nasby-Lucas 2013), and congregating near prey resources in coastal regions (*e.g.*, seal colonies; Kock et al. 2013). While white sharks are highly mobile, they also display a high degree of homing and seasonal philopatry to known aggregation sites (Domeier and Nasby-Lucas 2008; Jorgensen et al. 2010; Anderson et al. 2011; Domeier and Nasby-Lucas 2013).

Large mobile predators such as the white shark typically show some level of population connectivity (Bonfil et al. 2005; Taylor and Norris 2010). Mitochondrial DNA analyses, for example, have found some populations to be closely related (*e.g.*, Australia and New Zealand), while others are genetically distinct (*e.g.*, Australia-New Zealand versus South Africa; Pardini et al. 2001; O'Leary et al. 2015). The Atlantic population of white sharks historically included both the South African and the Northwest Atlantic (U.S. and Canada) populations (Andreotti et al. 2016). However, mitochondrial and nuclear genetic testing has revealed that Northwest Atlantic and South Africa white sharks are distinct populations, with the Northwest Atlantic population specifically showing signs of a strong genetic bottleneck effect (O'Leary et al. 2015). There is therefore recognized need for proactive management of the North Atlantic white shark population.

In Canada, species are managed by the Minister of Environment and Climate Change in partnership with the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) under the framework of the Species at Risk Act (SARA 2002). To be managed and assessed in Canada, a species must be divided into recognizable "*designatable units*", defined by COSEWIC as a "species, subspecies, variety, or geographically or genetically distinct population…where such units are both discrete and evolutionarily significant" (Environment and Climate Change Canada 2015). Given previous genetic testing, white sharks observed in Canadian waters are treated here as a designatable unit, distinguishable from the South African population (COSEWIC 2006; O'Leary et al. 2015). While a formal assessment and status report for the Atlantic Canada white shark designatable unit was undertaken more than a decade ago, the species was identified as "endangered", albeit rare, in Atlantic Canada waters, based on only 34 observations of white sharks off eastern Canada since 1874 (COSEWIC 2006). As a result, no action plan was established.

In the current study, we combine available sighting data (historical to present) on white sharks with recent satellite telemetry efforts in U.S. and Atlantic Canada waters to update the current status and distribution of this species in Canadian waters. We identify potential drivers of the occurrence of white sharks in Atlantic Canada and propose avenues of research for improved understanding of regional population dynamics. Finally, under the scenario of a relatively high, and/or potentially increasing presence of white sharks in Canadian waters, we present first considerations for an action plan for this species, given that the last review by COSEWIC was undertaken nearly 15 years ago.

METHODS

Collation of historical to present white shark sightings data in Atlantic Canada.

A systematic literature search was conducted to identify all relevant papers on the sighting or occurrence of white sharks in Atlantic Canada using standard academic and web-based search engines. Supplementary files from two key papers (MacPherson & Myers 2009 and Curtis et al. 2014) and the COSEWIC white shark assessment (COSEWIC 2006) provided the majority of historical records up until 1992 (n = 37). A recent report provided updated sightings between 1992 and 2016 (n = 23; DFO (2017)). All records were verified against the systematic literature search/internet reports. Associated metadata tied with shark sightings from the three main data sources were standardized and observations ranked in terms of level of confidence in recorded data (*i.e.*, if estimated size of animal was realistic; Supplementary Table S1). Duplication of sightings were checked and removed as necessary.

Shark capture, handling and satellite tag attachment

White sharks were captured by hook-and-line methods consisting of either modified individual drumlines or rod-and-reel with a baited 20/0 zero-offset circle hook, which was crimped to cable leader embedded inside polypropylene rope to minimize damage to the animal. A bite-blocker, consisting of a bamboo cross and/or bullet floats attached to the leader approximately 25 cm from the hook, prevented the bait from being swallowed and ensured the hook was set in the corner of the mouth. For targeting very large sharks (>400 cm TL) a baited 27/0 zero-offset circle hook was used.

Once caught, sharks were guided to the research vessel (M/V OCEARCH – 38m length) by a fishing crew operating from an 8.5 m fiberglass boat, using buoys attached to the leader as necessary to maintain the shark swimming near the surface. Each shark was then guided on to a submerged hydraulic platform (capability to lift 34,000 kg) and the lift was raised out of the water, allowing the shark to settle on the platform. The shark was provided with flowing seawater via a PVC tube and mouthpiece, a wet terrycloth towel was placed over the shark's eyes and gill slits to minimize stress, seawater was poured on the body to keep the skin moist, and a tail rope was attached to limit sudden movements. Morphometric measurements, and collection of samples for additional projects were then taken while the shark was equipped with satellite and acoustic electronic tags.

Smart Position and Temperature (SPOT) satellite tags (Wildlife Computers Ltd, Redmond, Seattle) were attached on the leading edge of the shark's first dorsal fin by drilling four holes through the fin with a cordless electric drill and attaching the tag with nylon bolts, stainless steel locknuts and plastic spacers. The attachment hardware is designed to retain the tag for its battery life, after which the hardware fails and the tag detaches. In all but one case (Shark ID 25), sharks were large enough to attach a five-year duration SPOT (WC model SPOT-257); shark 25 was outfitted with a one-year SPOT (WC SPOT-258) due to permit restrictions (Table 1). All tags were previously coated with an anti-fouling compound to reduce biofouling of the tags while attached to the animals.

Sharks were held on the hydraulic platform for ~15 - 20 minutes. For most of that period sharks rested on their left or right side depending on research procedures, then were turned upright onto their abdomen for SPOT attachment prior to release. Animal condition was monitored throughout the entire period by a marine veterinarian using objective behavioral and physiological criteria. At the conclusion of the protocol the platform was lowered, sharks swam off and post-release behavior was monitored. All activities were undertaken according to DFO Canada, U.S. NOAA, and state and provincial permits throughout the range of the study. All procedures were approved by the Jacksonville University IACUC and/or by IACUCs of individual collaborating organizations.

Telemetry data processing and analyses.

ARGOS location data derived from SPOT tags were extracted for each white shark that entered Canadian waters, with a focus solely on data that fell within or nearby the Canadian Exclusive Economic Zone (EEZ). Raw location data were first mapped to identify and remove locations that fell on land, and then a speed filter applied to remove unrealistic locations (argosfilter). A swim speed of 5 m/s was assumed for the filter, a liberal estimate, given the maximum swim speed of white sharks is ~2 m/s (Watanabe et al. 2019) and the adopted state-space model (SSM) is intended to control for measurement error. Prior to running the SSM, tag transmission data for each shark were divided into segments based on the time difference between locations to ensure there were no time gaps (*i.e.*, periods without transmissions) > 20 days. Given that white sharks can undergo periods without surfacing, this resulted in multiple tracks for individual sharks in instances where this conditions was met (Supplementary File S1 and Table S2). For white sharks with < 12 locations in Canadian waters, data for these individuals were not included in the SSM given it is not informative when based on few data. Raw transmission data, following the initial swim speed filter and removal of land transmissions, were used to document the tracks of these animals.

The *crawl* package was used to fit a continuous-time correlated random walk state-space model (hereafter SSM) to each white shark track, incorporating transmission location error based on ARGOS diagnostic data. The ARGOS ellipse-based 'location error' was used when feasible, and Argos 'location class' when error was not available. The first step of the SSM predicts the most likely daily locations for each shark based on raw transmission and error data. Given the fact that coastlines in Atlantic Canada are highly complex (i.e. multitude of islands) and the white shark commonly undertakes movements in close proximity to the coast, the second step of the SSM reiterates predicted tracks that cross land masses to circumnavigate the most likely coastal contour that constitutes the shortest distance movement. The final predicted daily locations per individual were then plotted by month of occurrence in addition to raw transmission data for sharks with <12 transmissions to examine the geographical and seasonal extent of white shark occurrence within Atlantic Canada and near the Canadian EEZ.

To further visualize the seasonal occurrence of white sharks within Atlantic Canada, the percent days detected in the Canadian EEZ by month was calculated for each individual shark using raw ARGOS locations (excluding those that fell on land or with a 0 or Z ARGOS location class). Raw filtered data were used to allow direct comparisons among all sharks, including those with limited geolocations to run the SSM. Each 'detection day' (defined as a day where one or more transmissions with valid locations were received for a shark) that fell within Canada's EEZ were summed for each individual per month. The total was then converted to a percentage based on the total number of days within that month. For sharks that returned to Canada across multiple years, percent (%) days detected individual^{-1} by month was calculated as an average across years present.

To identify core areas used by white sharks in Atlantic Canada and to provide a visual comparison between historical sightings and telemetry-derived locations, a kernel density plot of the SSM-corrected geolocations was generated using the geoprocessing tool Kernel Density in ArcGIS (ESRI, 2019). Individual geolocations were weighted equally, and the output cell size set to 9.2 km, with a search radius determined by Silverman's Rule of Thumb. The output density within each cell is a summation of the kernel surfaces that overlap that cell, resulting in higher values where numerous shark geolocations occur.

RESULTS

Historical to present sighting data

A total of 60 historical Atlantic Canada white shark observations from 1872 to 2016 were compiled from the literature. Of the 60 reported observations, 27 were sighted by observers, 26 were caught in fishing gear, and the remaining 7 were inferred from teeth left in fishing gear as well as wounds inflicted on seals and porpoises.

The prevailing perspective that white sharks are rare seasonal visitors to Atlantic Canada waters is based on historically infrequent sightings, which occurred every 5 to 10 years (Fig. 1a; McPherson and Myers 2009; Curtis et al. 2014), and inferential data such as slash wounds on seal carcasses, indicating seal predation (Lucas and Natanson 2010). Although a 3- to 950-fold decline in the white shark population within Atlantic Canada waters between any reference year from 1874–1988 and 2005 was estimated (McPherson and Myers 2009), recent sighting data suggest an increase in the occurrence of sharks since 2008, with a peak number of individuals recorded in 2016 (n = 9; Figure 1a). These sightings data indicate that white shark length (estimated total length; TL) in Atlantic Canada waters ranges from ~2–6 m (mean ± SD = 3.95 ± 1 m; Fig. 1c, Supplementary Table S1; unauthenticated lengths excluded) including older juvenile, sub-adult and mature animals. Sightings (n = 29; 48%) peaked in August, indicating seasonality of white shark presence (Fig.1b). In addition, sightings indicate white sharks primarily occur in the Bay of Fundy (n = 28), off the coast of southwest Nova Scotia (n = 15), and off Sable Island (n = 3; Fig. 2), with an average of 2 sightings year^{-1} across years in which sharks were observed (Fig. 1a). Aside from these hotspot areas, sightings of white sharks have occurred as far north as Newfoundland and on the coast of Québec along the St. Lawrence seaway (Fig. 2; McPherson and Myers 2009).

Satellite telemetry data

Between 2013 and 2019, a total of 18 large juvenile, sub-adult and adult white sharks were equipped with Smart Position or Temperature Transmitting Tags (SPOTs; Wildlife Computers Ltd, Redmond, Seattle) in U.S. Atlantic waters during OCEARCH expeditions (off Massachusetts, n = 11; South Carolina, n = 5; and Florida, n = 2; TL range: 2.5–4.9 m; Table 1). Nine of these sharks (50%) entered Canadian waters with derived geolocations distributed across the majority of coastal and offshore waters within the exclusive economic zone (EEZ) south of Newfoundland (Fig. 3a) and entering the high seas. Tag transmissions in Atlantic Canada occurred predominantly between the months of June and February; seven individuals were present between June and November, three individuals were recorded in December, two sharks in January and one shark in February (Fig 3a,e; Supplementary Table S1). Three individuals returned to Atlantic Canada over two years (Shark ID 5 [male; 3.79m Total Length (TL)]; Fig. 3c, Shark ID 2 [female; 3.84m TL and Shark ID 4 [male; 3.00 m TL]; Supplementary Table S2), while a large female shark (Shark ID 1 [4.42m TL]) returned across three years (Table 1; Supplementary Table S2).

In 2018, a total of six white sharks were caught and tagged at West Ironbound Island, Nova Scotia, during 17 days of active fishing between 20 September and 9 October (four additional sharks were observed, but were not captured and another was captured, measured, sampled and released without a tag due to permitting restrictions at that time; catch per unit effort [CPUE] = 0.0076 sharks hook-hour^{-1}; Supplementary Table S3). In 2019, a total of eleven sharks were captured and tagged at Scatarie Island in Cape Breton (n = 3) and west Ironbound Island (n = 8) during 19 days of active fishing between 14 September and 4 October (five additional sharks were observed, but not captured; estimated CPUE = 0.0084 sharks hook-hour^{-1}; Supplementary Table S3). Sharks captured in Atlantic Canada included both large juveniles, sub-adults and mature animals (TL range: 2.5–4.3 m) and both sexes (6 females and 11 males; Table 1). White shark tag transmission data over the two-year period were centered around southern Nova Scotia, including the Bay of Fundy (Fig. 3b and accepting the bias associated with animals being captured and tagged in this location). All six white sharks tagged off Nova Scotia in 2018 returned to the region in 2019 (Supplementary Table S2). Sharks demonstrated site fidelity, with shark ID 10 (male; 2.74m TL) returning to the southern peninsula of Nova Scotia (Fig 3d), shark ID 12 (female; 4.25m TL) returning to the Bay of Fundy, and shark ID 9 (male; 3.90m TL) detected < 3 km from its original capture location 10.5 months post-release (recorded via pop-off location of a pop-up archival satellite tag [PSAT; Wildlife Computers Ltd, Redmond, Seattle]). When considering only the return year (*i.e.*, removing bias associated with capture/tagging, and the potential for sharks to migrate out of a region post-capture), sharks were present in Atlantic Canada between June and October inclusive, with the highest number of individuals detected in July and August (Fig. 3e). White sharks remained on average 45 ± 47 days (mean ± SD; range: 1 – 119 d; n = 6); however, there was evidence of only two sharks exiting Canadian waters within this timeframe, suggesting this likely does not encompass the entire period sharks were present within Atlantic Canada waters.

Combined, U.S. and Canada-tagged white sharks entered and exited the Canadian EEZ via both continental shelf and pelagic waters (Fig. 3a, b). The focal hotspot of white shark occurrence, based on kernel density estimation of interpolated track data, encompassed the coastal region along the southeastern coast of Nova Scotia and extending in to the Bay of Fundy, an area where a large number of historical sightings were recorded (Fig. 2). A secondary hotspot occurred in southern coastal and offshore waters around Newfoundland including the Grand Banks (Fig 2, 3a and 3c). The hotspot for the latter location, however, was influenced by intense tracks of a few individual sharks.

DISCUSSION

The size range of white sharks, timing of occurrence, and focal areas used in Atlantic Canada expands on initial tagging data presented by Skomal et al. (2017) for sharks tagged off Massachusetts. The recent, increasing trend in sighting data of white sharks in Atlantic Canada also matches that reported in Massachusetts and the US north Atlantic (Skomal et al. 2012; Curtis et al. 2014). The frequency of U.S.-tagged sharks entering Canadian waters, and the successful targeted capture and tagging of multiple white sharks off Nova Scotia over two consecutive years, indicate seasonal, inter-annual presence of white sharks in Canadian waters and higher regional frequency and abundance than previously thought.

Distribution and population trends of the white shark in the northwest Atlantic

Until recently, our understanding of white shark distribution in U.S. Northwest Atlantic waters relied mostly on data collected through opportunistic sightings and catches (Casey and Pratt 1985; Curtis et al. 2014). White shark sightings primarily ranged from New England to Florida in water temperatures between 14–23°C, with most restricted to the continental shelf (<200 m depth; Curtis et al. 2014). Of sightings recorded in the Gulf of Mexico, the majority occurred in winter and spring between January and June (Casey and Pratt 1985; Curtis et al. 2014). This contrasts with sightings in Atlantic Canada, which primarily occur between May and September (Fig. 1b). Collectively, these data suggest that white sharks move to waters off the southeastern U.S., with some moving into the Gulf of Mexico, during the winter and early spring when water temperatures drop below 22°C in the Northwest Atlantic (Adams et al. 1994). These marked seasonal movements have recently been verified using satellite telemetry (n = 31 individuals tagged with PSATs off Cape Cod, Massachusetts and n = 1 off Jacksonville, Florida) (Skomal et al. 2017).

White shark populations in the U.S. North Atlantic are reported to have declined significantly through the 20th century (Baum et al. 2003; but see Burgess et al. 2005). Recent evidence, however, suggests that the population has been recovering since the early 1990s (Curtis et al. 2014), with a 26% increase in shark observations off Massachusetts between 1990 and 2009, corresponding with the recovery of the grey seal (*Halichoerus grypus*) population (Skomal et al. 2012). The population recovery of white sharks off Massachusetts is circumstantially corroborated by the recent increase in Atlantic Canada sightings between 2010–2016 (Fig. 1a).

Potential scenarios for current white shark occurrence and abundance in Canadian waters

The apparent abundance and/or distribution of white sharks in Atlantic Canada (Fig. 2) presents two alternative, but not mutually exclusive, scenarios: 1) white sharks have been historically abundant seasonally in Canadian waters, and recent focused studies and technological advances have allowed for research to demonstrate this; or 2) white shark abundance and/or residency duration in Canadian waters has increased. A northward range expansion could be related to multiple factors, including warming Canadian waters due to climate change, population recovery, and/or increased regional prey abundance.

The previously low number of white shark sightings in Atlantic Canada waters could be due to poor or incomplete historical data (Curtis et al. 2014). Lack of sightings may relate to inadequate sampling in certain habitats (remote or difficult to access areas, *e.g.,* offshore waters) or depths (*e.g.,* Skomal et al. 2009), public inability to correctly identify white sharks (*e.g.,* Rankin et al. 2007), or poor environmental conditions that result in low sighting accuracy and observational effort (*e.g.,* Theberge and Dearden 2006; Rankin et al. 2007). In recent years, the general public has become more involved with the scientific community through citizen science programs (Silvertown 2009; LaRue et al. 2019). These programs are promoting the rapid growth of megafauna sighting datasets with greater spatial coverage (*i.e.* increased spatio-temporal effort; Devictor et al. 2010; LaRue et al. 2019) for numerous pelagic species (*e.g.,* minke whales, Rankin et al. 2007; and manta rays, O'Malley et al. 2013). In addition, fishing methods have become more efficient over the past three decades (Kennelly and Broadhurst 2002), covering larger areas and increasing in intensity, resulting in higher levels of shark bycatch (Dulvy et al. 2014; Queiroz et al. 2019). Based on compiled shark sightings between 1872 and 2016, "free swimming" sharks were reported more frequently in earlier years, while sharks reported as bycatch were more common in later years (Supplementary Table S3). The ability to track white sharks for multiple years with electronic tagging technology far surpasses the ability to otherwise observe white sharks, which seem to be particularly cryptic in Canadian waters. This presents the possibility that tag-demonstrated yearly aggregations of white sharks in Atlantic Canada may have been occurring over historical timeframes, as confirmed historical sightings date back to 1872. This underscores the importance of telemetry studies, since a large, highly mobile, predatory shark may have been historically abundant in Canadian waters, yet considered 'rare' simply due to our inability to observe them.

A northward range shift or expansion of habitat use by Atlantic white sharks is also possible, which may be partially explained by climate change. White sharks are most frequently sighted in Canadian waters during summer months (Fig. 1b), when the southerly waters of the U.S. are above the sharks' preferred temperature range of 14–23°C (Curtis et al. 2014). Climate change is a known driver of marine fish redistributions, particularly in areas experiencing rapidly warming temperatures (Perry et al. 2005; Cheung et al. 2009; Pinsky et al. 2013). In North Atlantic waters, sea surface temperatures have increased by 0.11°C decade^{-1} (IPCC 2014), triggering changes in abundance, range, phenology, and body size of local marine fauna (Kavanaugh et al. 2017), and is projected to further increase by 1.4–5.8°C over the next century (Arbic and Brechner Owens 2001; Belkin 2009; Taboada and Anadón 2012; Saba et al. 2016). An increase in Atlantic Canada white shark sightings in recent years may therefore be the result of white sharks seeking cooler northern waters during the warm summer months (Fig. 1a; Day and Fisher 1954; Mollomo 1998; Turnbull and Dion 2012). A white shark distribution shift may also be influenced indirectly by climate change due to shifts in prey abundance in response to changing water temperatures (Robinson et al. 2009).

Such effects of climate change on predator distribution ranges have been well documented. For example, sightings of the striped dolphin (*Stenella coeruleoalba*) off northwest Scotland have doubled since 1998 as a result of a northward movement, replacing the historically dominant white-beaked dolphin in the region (MacLeod et al. 2005; MacLeod 2009). Similarly, the gray whale (*Eschrichtius robustus*) was recently recorded in the Mediterranean Sea (Scheinin et al. 2011). Marine ectotherms, such as demersal fish assemblages of cod, anglerfish, and snake blenny are also experiencing northward range shifts (Perry et al. 2005), while climate-driven alterations in migratory routes and spatial distribution have been noted in regional endotherms such as the Atlantic bluefin tuna (*Thunnus thynnus*) (e.g. Robinson et al. 2009). In the Northeast Atlantic, killer whales (*Orcinus orca*) have moved northward from the Norwegian Sea into Arctic waters in pursuit of northward shifting prey (Moore and Huntington 2008). It is plausible that Atlantic white sharks may be responding to similar prey distribution shifts driven by climate change.

The apparent increase in white sharks in Atlantic Canada waters could also result from either a population recovery due to effective conservation measures in the U.S. and/or a response to increasing prey abundance, *i.e.* driven by recovering seal populations (Bowen et al. 2003). Four species of seal are commonly found in eastern Canadian waters, all documented prey of white sharks. Two species of seal are resident year-round: the harbour seal (*Phoca vitulina*) and the grey seal (Dubé et al. 2003). The harp seal (*Phoca groenlandica*) and hooded seal (*Cystophora cristata*) are migratory and can be found in eastern Canada waters from December to May (Lucas et al. 2003; Dubé et al. 2003). The two resident seal populations, harbour and grey seals, have both experienced population growth and recovery in recent decades.

White shark predation on harbour seals in the Maritimes has been reported, particularly around Sable Island, Nova Scotia (Boulva and McLaren 1979; Brodie and Beck 1983), with predation typically intensifying during the late summer and early autumn months (Boulva and McLaren 1979). Historically, the harbour seal population in the region has fluctuated through time, though the overall trend indicates an increase in population from 1949 to present (Hammill and Stenson 2000; DFO 2016). Following the termination of a harbour seal hunt and bounty program, which was in place until the early 1970s (DFO 2016), abundance of seals increased from ~23,000 in the 1990s to ~32,000 in 1996 (Hammill and Stenson 2000). A more recent 2010 minimum estimate of the total population, including all ages, is between ~8,000–12,000 individuals on Sable Island, ~4,000–5,000 in the Gulf and estuary of the St. Lawrence, and ~4,000–7,000 in the Bay of Fundy (Hammill et al. 2010); DFO currently estimates there to be ~20,000–30,000 harbour seals in Atlantic Canada (DFO 2016). While sightings of sharks actively preying on harbour seals are still relatively rare (Day and Fisher 1954; Turnbull and Dion 2012), there has been a noted increase in harbour seal carcasses and an increase in seals with wounds (Lucas and Stobo 2000; Lucas and Natanson 2010). The grey seal, an important prey species for white sharks off Massachusetts, has experienced exponential population growth since 1960, from ~13,000 to 410,000 in 2010 (Skomal et al. 2012). A 2014 population modelling study based on survey data of the northwest Atlantic grey seal populations on Sable Island, coastal Nova Scotia, and the Gulf of St. Lawrence during the breeding season found that there has been a continuous increase in population size over time, with an estimated current total population of ~505,000 (Hammill et al. 2014).

Marine apex predators such as killer whales have been documented to increase the probability of calving in response to prey abundance (Ward et al. 2009). It is therefore possible that with greater prey availability, white sharks are experiencing a similar increase in fecundity and survival rates. An increase in shark sightings in Atlantic Canada due to an increase in the local seal population would mirror that observed in Massachusetts (Skomal et al. 2012).

Proposed Action Plan for White Shark Conservation and Management in Atlantic Canada

White sharks have not been considered a species in need of active management in Canada (COSEWIC 2006). However, historical to present sightings and recent telemetry data presented here demonstrate a substantial, regional and seasonally consistent white shark presence in Atlantic Canada. We recommend a precautionary approach to develop a management plan for white sharks in Atlantic Canada, one that considers adaptive conservation measures in the face of climate change (Pecl et al. 2017), identifies knowledge gaps and research priorities, and assesses current legislation protecting this species. Successful management of the white shark will balance public opinions on its presence and conservation in Atlantic Canada to ensure responsible approaches to human-shark interactions and anticipate the potential for human-shark conflicts (Simpfendorfer et al. 2011; Christie et al. 2017). We outline a proposed action plan that includes the following components; (1) prioritizing improved public awareness and education of white shark conservation issues and perception of the species; (2) quantifying multi-year distribution, seasonality, population size, and environmental health of white sharks in Atlantic Canada through focused research efforts; (3) promoting/enforcing responsible fisheries management practices; and (4) establishing relevant protective legislation in Canadian EEZ waters with consideration of the need for marine protected areas relevant to white shark core habitat use and identifying shark-human interaction hotspots (Table 2).

1. Prioritizing public awareness

The public perception of white sharks is often negative due to attacks on humans and anti-shark media, leading to reduced support for conservation actions (Muter et al. 2013; Bornatowski et al. 2019). In terms of fatal shark attacks on humans when the species of shark can be identified, white sharks are responsible for the most fatalities (ISAF 2018). This may lead to support for lethal measures for shark control following serious human-shark interactions (Pepin-Neff and Wynter 2018). In Australia, however, there has been overwhelming public support for non-lethal measures of shark control following campaigns to educate the public of conservation issues and potential actions to mitigate conflicts (Pepin-Neff and Wynter 2018). Therefore, increased education is necessary to raise public awareness for shark conservation and to foster positive public shark perceptions in Canada (Simpfendorfer et al. 2011; O'Bryhim and Parsons 2015). Following recent lessons learned in Cape Cod as a result of direct human-white shark interactions, it will be prudent to both implement more stringent public safety measures in identified hotspots (*e.g.* increased life guard presence, relevant first aid training, beach medical response supplies and signage and safety protocols) and to consider technology-based shark mitigation measures (see Woods Hole Group 2019 for detailed recommendations).

2. Quantifying population distribution and size

Current distribution and abundance data for the white shark in Canadian waters inadequately represents its true range and seasonality, as it is based primarily on data collected through rudimentary sighting techniques (Curtis et al. 2014). Telemetric approaches (*i.e.* satellite, acoustic and biologging tags) can provide accurate, continuous location data on the spatial and temporal distribution of white sharks in Canadian waters, allowing researchers to more accurately determine movement behaviors, monitor change and predict future patterns (Bonfil et al. 2005; Hussey et al. 2015), and also to assess survivorship rates and population size (Block et al. 2019; Lees et al. In revision). The use of PSATs with integrated pressure/temperature sensors deployed on four Canadian white sharks to date as part of the OCEARCH program will provide diving profiles of individuals, with associated ambient temperature data, to understand the vertical thermal regimes encountered. These data will further our understanding of the physiology and ecological role of this species in Canadian waters and complement current efforts underway by DFO to derive PSAT data for this species (two tags deployed to date). Overall, movement data (e.g. increased sample size and long-term monitoring) and advanced techniques (e.g. kernel density estimators that account for autocorrelation; Fleming and Calabrese (2016)) will build on these initial findings to allow continued assessment of hotspot regions (vertical and horizontal) that can be managed in a sustainable manner for both shark and human needs (Heupel et al. 2015). Specifically, with increasing white shark abundance, these data will highlight coastal regions where there is the potential for high human-shark conflict and allow experts to assess the current status of marine protected or conservation areas and if considered necessary designate new areas appropriate for white shark management. Consideration of new conservation or marine protected areas, however, must involve consultation with all stakeholders that could be potentially impacted. In addition, studies of the environmental health of white sharks in Atlantic Canada are required to assess population fitness and resilience to ongoing climate change and environmental threats such as marine pollution. Understanding the ecological role of this apex predator species, through improved knowledge of predator-prey interactions (via direct observation and biotelemetry techniques such as biologging) and the application of chemical tracers (e.g. stable isotopes and fatty acids) to document diet and trophic shifts will be needed for accurate ecosystem assessment and management. National and provincial funding for focused white shark research from research council, government, and non-government sectors should be prioritized to address knowledge gaps and to enhance conservation and management efforts.

3. Promoting responsible fisheries

Recreational and commercial fishing can negatively impact marine organisms at all trophic levels (Pauly et al. 1998; Cooke and Cowx 2004; Pauly and Zeller 2016). Sharks are particularly susceptible to fisheries exploitation due to late ages of maturity, slow growth rates, and low fecundity (Morgan and Burgess 2007; Dulvy et al. 2014), with estimated catch rates (including bycatch) often exceeding rebound rates and contributing to population declines (Worm et al. 2013). Certain fishing gears result in increased susceptibility of accidental capture of larger individuals, particularly pelagic longlines (Oliver et al. 2015; Queiroz et al. 2019). While white sharks are not a species typically considered at risk of high bycatch in commercial fisheries (but see Baum et al. 2003), accurate data to assess this are not available. Following a precautionary approach, it will be advisable for managers to work closely with the fishing industry to establish protocols for accurately reporting white shark bycatch (*e.g.*, location, date, basic data on size and sex) (Glass et al. 2015). Moreover, given the increasing presence of white sharks in Atlantic Canada, it would seem prudent to consider options for modifying fisheries gear to limit white shark bycatch, and to establish handling and release protocols to minimize mortality if encountered. Continuing work on mitigating shark bycatch in Atlantic Canada waters following initial trials (Godin et al. 2013) is required for other large pelagic species (*e.g.* blue [*Prionace glauca*], shortfin mako [*Isurus oxyrinchus*] and porbeagle [*Lamna nasus*]) as well as white sharks. For recreational fisheries, targeting of the species should not be allowed in either recreational or commercial fisheries, though incidental catch-and-release may occur.

4. Relevant species protective legislation and protected areas

The responsible management of white sharks in Atlantic Canada is the obligation of several regulatory bodies. These include international agencies and treaties such as the International Union for Conservation of Nature (IUCN), the Northwest Atlantic Fisheries Organization (NAFO), Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), Convention on Biological Diversity (CBD), and Convention on Migratory Species of Wild Animals (CMS). At the federal level in Canada, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Species at Risk Act (SARA), Department of Fisheries and Oceans (DFO), Environment and Climate Change Canada (ECCC), and the Canadian Endangered Species Conservation Council are responsible for regulations governing wildlife. In addition, non-governmental organizations, such as the National Resources Defense Council (NRDC), World Wildlife Fund (WWF), Wildlife Conservation Society (WCS) and Sharks of the Atlantic Research and Conservation Centre (SHARCC) could play key roles advocating for the management of white sharks during the public consultation in the COSEWIC and SARA listing process. OCEARCH, a U.S.-based nonprofit research and education organization, has already made significant inroads in outreach to the Canadian public through two expeditions to Nova Scotia in 2018-2019 during which people were able to visit the research vessel and speak with staff over scientific activities underway. In addition, OCEARCH provides open access to resulting white shark satellite tracks through their website (www.ocearch.org) and OCEARCH Tracker free app for smartphones. Effective communication and collaboration among all stakeholders will be essential to ensure the successful implementation of a proactive management strategy for white sharks in Atlantic Canada.

The current state of regulations and associated legislation for white sharks in Canadian waters is limited. In the early 2000s, CITES listed the white shark in Appendix II, which requires close monitoring of trade in meat and by-products (e.g. fins, jaws). In U.S. federal waters, white sharks are on the "prohibited" species list and cannot be retained, although there are no regulations against targeting the species in catch-and-release recreational fisheries (see www.fisheries.noaa.gov). While the IUCN and DFO consider the white shark vulnerable (Rigby et al. 2019) and endangered in Atlantic Canada waters (COSEWIC 2006), respectively, currently no federal or provincial laws directly protect this species (COSEWIC 2006). This contrasts with the Pacific population of white sharks that have limited protection, with laws preventing hook-and-line fisheries from keeping any sharks except spiny dogfish (*Squalus acanthias*; COSEWIC 2006). Considering the consistent seasonal occurrence of white sharks in Atlantic Canada demonstrated here, exploration of effective and preemptive management of this species beyond current legislation with relevant stakeholders is a necessity. Quantifying white shark spatial overlap with current marine conservation areas and identifying risk areas based on proximity of white sharks to recreational and commercial human population centers and core water usage areas will also be necessary to sustainably manage this iconic species.

Conclusion

Sighting and satellite telemetry data indicate a potential recent increase, and apparent seasonal abundance, of white sharks in Atlantic Canada. This presents new challenges to manage this species and mitigate potential detrimental effects resulting from unintended shark-human interactions. The rebuilding of the white shark population off Massachusetts (Skomal et al. 2012) and the recent shark attack in Cape Cod, which negatively shifted local public opinion of white sharks, emphasize the importance of a clear action plan and need for both data and education to limit negative interactions and promote awareness and conservation. This will need to be a coordinated and collaborative effort that includes researchers, policy makers, non-governmental organizations and the general public. Actions recommended here will ensure adequate protection for white sharks and their associated ecosystems, given their role as a top predator and their current SARA listing of "endangered" in Atlantic Canada waters (COSEWIC 2006). Whether the consistent seasonal presence of white sharks in Canadian waters had previously gone unknown or is a result of population recovery**,** a northward shift related to increasing ocean temperatures, and/or increased abundance of marine mammal prey requires further investigation.

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FIGURES:

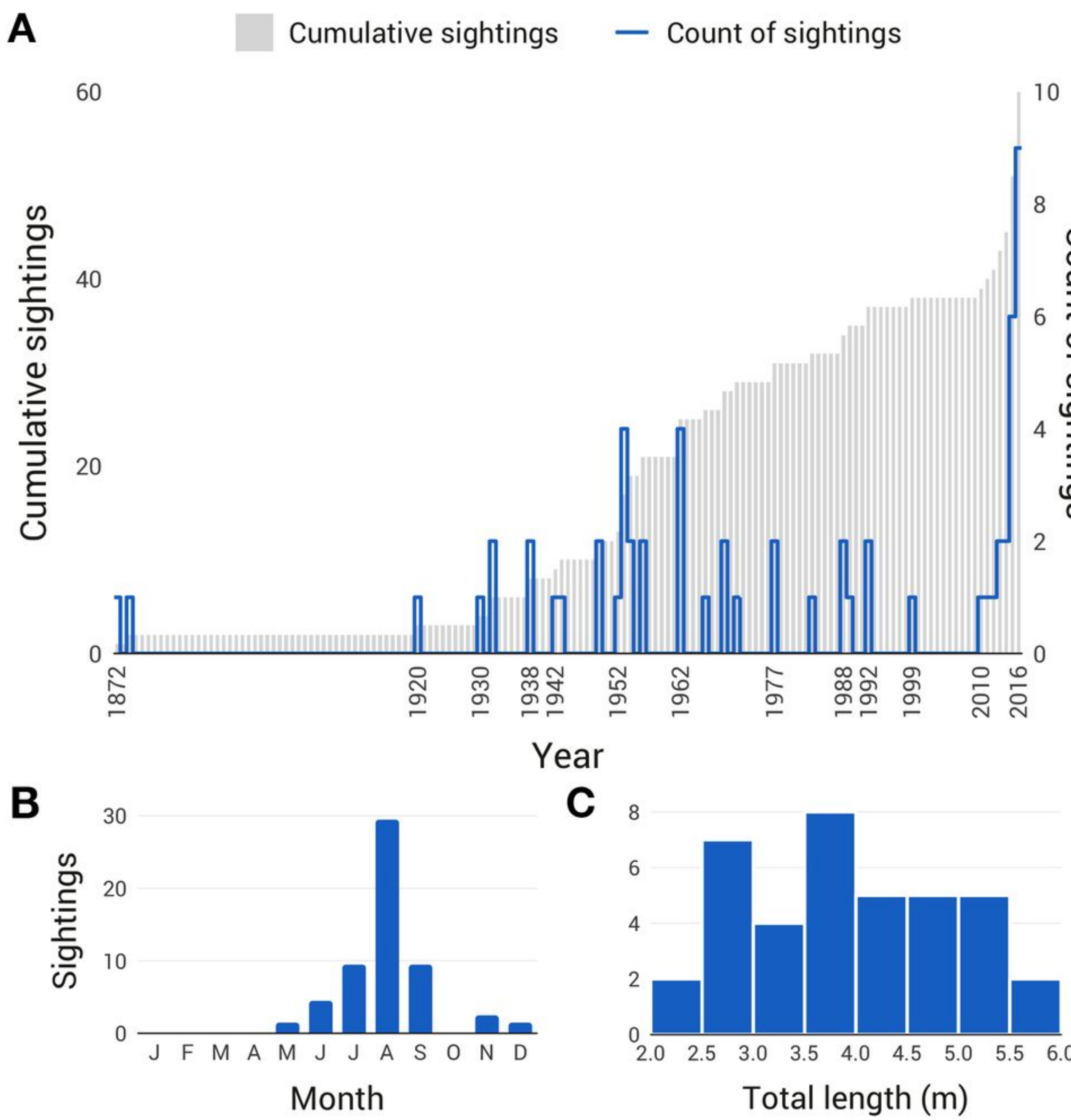

Figure 1. Synthesis of historical to present white shark sightings in Atlantic Canada. (**A**) Counts and cumulative white shark sightings in Atlantic Canada waters from 1872–2016 (n = 60 total sightings). (**B**) Monthly distribution of white shark sightings in Atlantic Canada (total n = 55; unreliable records excluded). (**C**) Length distribution of white sharks sighted in Atlantic Canada (n = 38; includes only sharks with verified length information). See Supplementary file S1 and Table S1 for details on data.

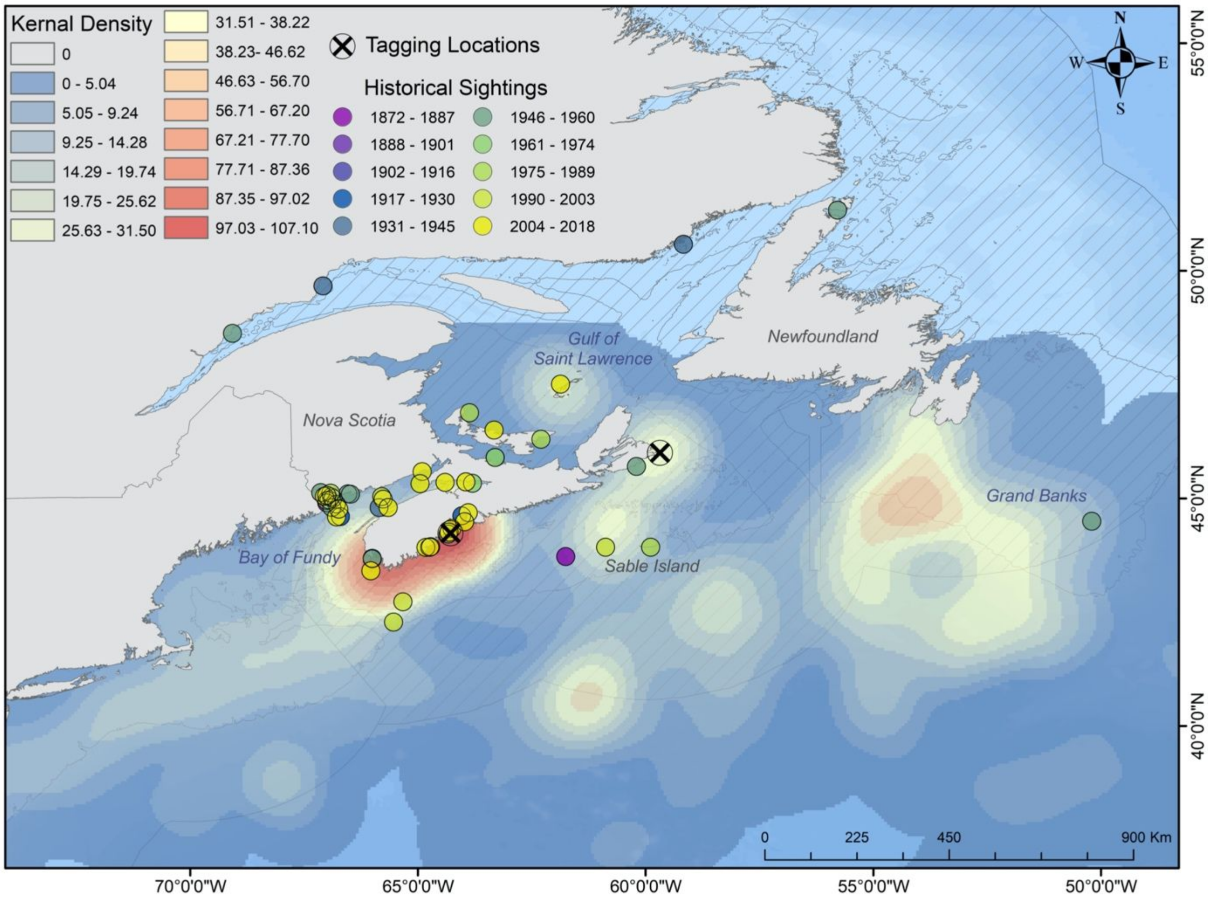

Figure 2. Distribution and hotspots of white sharks in Atlantic Canada waters derived from sightings and telemetry data. Circles show historical to present distribution of white shark sightings in Atlantic Canada waters from 1872 to 2016 (colored by year of sighting). Sightings include visual observations of animals in water (*n* = 27), capture in fishing gear (*n* = 26) and teeth in fishing gear/wounds on marine mammals (*n* = 7). Underlying map indicates high core area use of all satellite-tracked white sharks tagged in US and Atlantic Canada waters to date, based on kernel density estimation. Hashed area demarcates the Canadian Economic Exclusive Zone (EEZ; Flanders Marine Institute 2020). Map created in ArcGIS (ESRI 2020) using bathymetry and derived contour lines from GEBCO Compilation Group (2020) and shorelines from GSHHG (2017).

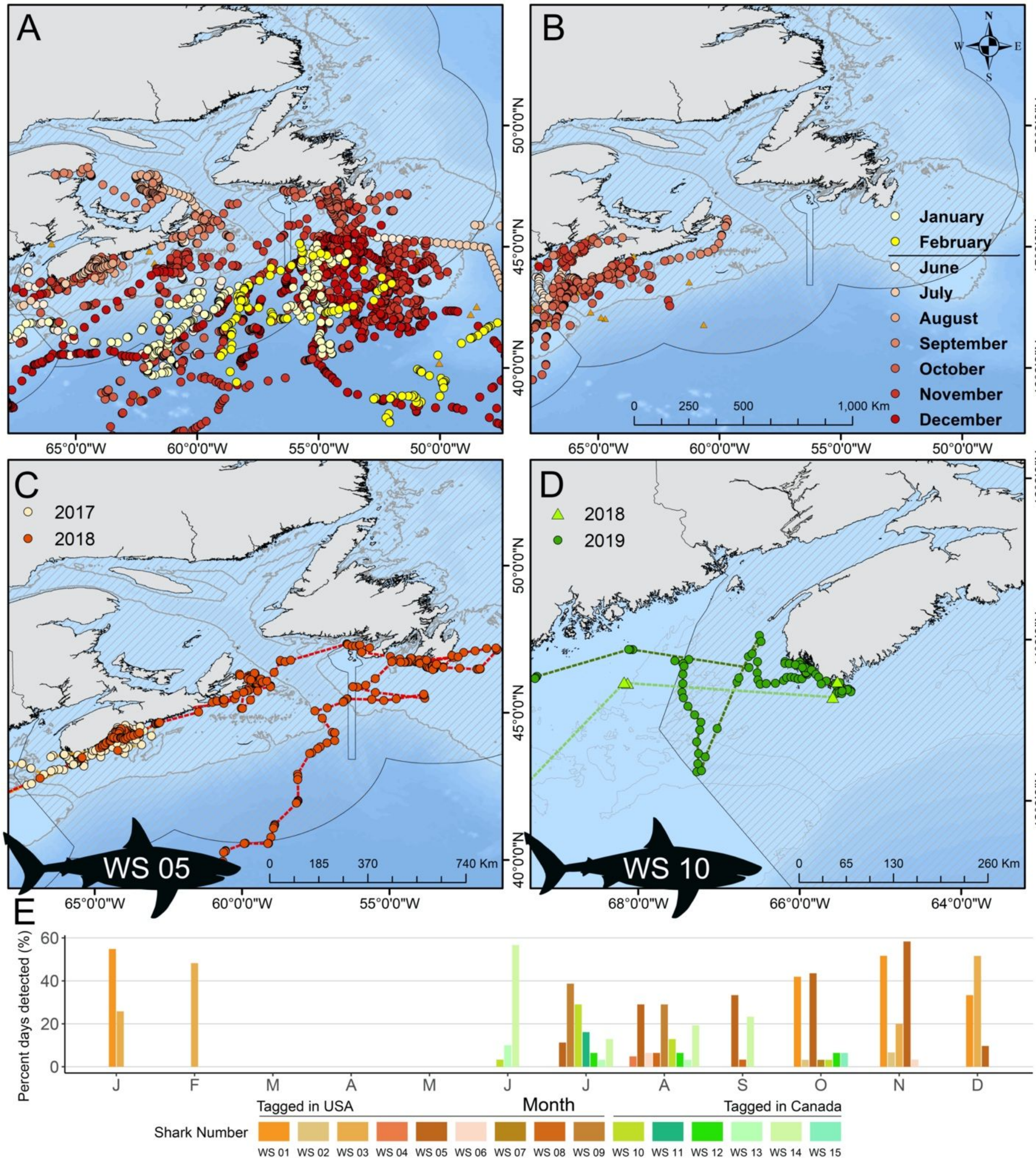

Figure 3. Spatial-temporal distribution of all white sharks equipped with SPOT satellite transmitters recorded in Atlantic Canada waters. (**A**) Satellite tracks of nine white sharks tagged in U.S. waters that entered Atlantic Canada (n = 9), **(B)** Satellite tracks of 17 white sharks

tagged in Canadian waters in 2018 (n = 6) and 2019 (n = 11). (**C**) tracks of Hilton (tagged in US waters) and (**D**) Cabot (tagged in Atlantic Canada waters) that exited and returned to Canadian waters over a two-year period. All locations are those estimated using a continuous time correlated random walk state-space model with the exception of the 2018 track for Cabot (shown as triangles in D), which shows geolocated positions due to the limited sample size (See Methods) (**E**) Number of days that transmissions were received each month (calculated as a percentage; days month^{-1}) for each individual white shark present in Atlantic Canada waters (labelled by those tagged in both US and Canadian waters). Hashed area demarcates the Canadian Economic Exclusive Zone (EEZ; Flanders Marine Institute 2020). Map created in ArcGIS (ESRI 2020) using bathymetry and derived contour lines from GEBCO Compilation Group (2020) and shorelines from GSHHG (2017).

Table 1: Metadata for all white sharks equipped with SPOT satellite transmitters that entered or were tagged in Atlantic Canada waters. ID is the assigned identification number, latitude and longitude indicate the exact location of tagging, TL is total length in meters, F and M refer to female and male, respectively.

Name	ID	Tag Date	Latitude	Longitude	TL (m)	Sex	Capture location & Country
Lydia	1	2013-03-03	30.39	-81.38	4.42	F	Florida, USA
Betsy	2	2013-08-13	41.69	-70.30	3.84	F	Massachusetts, USA
Katharine	3	2013-08-20	41.69	-70.30	4.32	F	Massachusetts, USA
George	4	2016-10-07	41.49	-69.98	3.00	M	Massachusetts, USA
Hilton	5	2017-03-03	32.09	-80.57	3.79	M	South Carolina, USA
Savannah	6	2017-03-05	32.23	-80.63	2.60	F	South Carolina, USA
Nova	7	2018-09-24	44.23	-64.28	3.41	M	Nova Scotia, Canada
Jefferson	8	2018-09-24	44.23	-64.28	3.86	M	Nova Scotia, Canada
Hal	9	2018-09-29	44.23	-64.28	3.90	M	Nova Scotia, Canada
Cabot	10	2018-10-05	44.23	-64.28	2.74	M	Nova Scotia, Canada
Jane	11	2018-10-08	44.23	-64.28	2.86	F	Nova Scotia, Canada
Luna	12	2018-10-08	44.23	-64.28	4.25	F	Nova Scotia, Canada
Helena	13	2019-02-22	32.06	-80.42	3.79	F	South Carolina, USA
Brunswick	14	2019-02-26	32.00	-80.59	2.66	M	South Carolina, USA
Caroline	15	2019-02-26	32.00	-80.59	3.88	F	South Carolina, USA
Sydney	16	2019-09-15	46.02	-59.68	3.71	M	Nova Scotia, Canada
Murdoch	17	2019-09-16	46.00	-59.68	3.93	M	Nova Scotia, Canada
Unama'ki	18	2019-09-20	46.02	-59.68	4.33	F	Nova Scotia, Canada
Caper	19	2019-09-26	46.04	-59.69	2.50	F	Nova Scotia, Canada
Bluenose	20	2019-09-29	44.23	-64.28	3.53	F	Nova Scotia, Canada
Ferg	21	2019-09-30	44.23	-64.29	3.32	M	Nova Scotia, Canada
Shaw	22	2019-10-01	44.23	-64.29	2.88	M	Nova Scotia, Canada
Scotia	23	2019-10-01	44.23	-64.28	3.13	F	Nova Scotia, Canada
Ironbound	24	2019-10-03	44.23	-64.29	3.46	M	Nova Scotia, Canada
Teazer	25	2019-10-03	44.23	-64.29	3.13	M	Nova Scotia, Canada
Vimy	26	2019-10-04	44.23	-64.28	3.63	M	Nova Scotia, Canada

Table 2. Outline of Atlantic Canada white shark (*Carcharodon carcharias*) management priorities and conservation goals**.**

Objective 1: Positive public awareness and perception of white sharks	**Action 1:** Enhance social media presence of white shark science underway and associated researchers/organizations
	Action 2: Promote balanced white shark coverage in Canadian broadcasting and news media
	Action 3: Increase white shark public education programs (targeting schools, general public, and specifically recreational and commercial water users, *e.g.*, surfers and fishers)
Objective 2: Improved scientific knowledge	**Action 1:** Identify seasonal/yearly movement and migration patterns in Canadian waters
	Action 2: Long-term monitoring to determine the stability of identified "hotspot" habitat in Atlantic Canada and quantify associated environmental and prey resources
	Action 3: Estimate population size and survivorship parameters
	Action 4: Derive health and condition data to monitor population status
	Action 5: Determine ecological role to facilitate ecosystem level management

Objective 3: Responsible proactive fisheries management	**Action 1:** Limit shark bycatch in commercial fisheries and maintain a zero landings limit for all fisheries
	Action 2: Prohibit targeting of white sharks in recreational and commercial fisheries
	Action 3: Invest in active research and trials to support gear modification to reduce shark bycatch and development of best handling practices for releasing large sharks
	Action 4: Improve reporting of bycatch by fisheries (location, size, weight, sex)
	Action 5: Ensure ban on trade of white shark products is enforced
Objective 4: Appropriate legislation and consideration of human-shark conflict	**Action 1:** Coordinate re-evaluation of white shark status and enact required species legislation with broad stakeholder involvement
	Action 2: Assess variation in spatial distribution of white sharks relative to current marine protected/conservation area network, and modify, expand, or create new conservation/protected areas and associated legal frameworks to include white shark-specific criteria

	Action 3: Determine proximity of white shark occurrence to human coastal settlements, prime areas used by recreational water users, and overlap with fisheries
	Action 4: Assign potential risk in human-shark conflict areas, ensure awareness of general public and implement public safety measures