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Movement ecology of the Greenland shark (*Somniosus microcephalus*): Identifying tools, management considerations, and horizontal movement behaviours using multi-year acoustic telemetry

By

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Movement ecology of the Greenland shark (*Somniosus microcephalus*): Identifying tools, management considerations, and horizontal movement behaviours using multi-year acoustic telemetry

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DECLARATION OF CO-AUTHORSHIP/PREVIOUS PUBLICATION

I. Co-Authorship

I hereby declare that this thesis incorporates material that is result of joint research which was undertaken under the supervision of Dr. Nigel Hussey in all cases. Two published reviews are included in the general Introduction, followed by unpublished co-authored manuscripts in Chapters 1 and 2. The first introductory review was co-authored by J.E. Edwards, E. Hiltz, F. Broell, P.G. Bushnell, S.E. Campana, J.S. Christiansen, B.M. Devine, J.J. Gallant, K.J. Hedges, M.A. MacNeil, B.C. McMeans, J. Nielsen, K. Præbel, G.B. Skomal, J.F. Steffensen, R.P. Walter, Y.Y. Watanabe, D.L. VanderZwaag and N.E. Hussey. For this manuscript, the author was responsible for contacting and coordinating the collaborating authors, as well as writing the Abstract, Introduction, Methods, and Movement Ecology section (alongside N.E Hussey), composing tables and figures, and conducting final edits. Co-authors contributed to the general outline (composed by E. Hiltz), wrote the remaining subsections, and provided additional edits for the overall submission.

The second introductory review was co-authored by J.E. Edwards, J. Pratt, N. Tress, N.E. Hussey. Co-authors contributed to the main ideas as well as the original literature search and review of primary sources, while the author was responsible for conducting additional literature searches, reviewing sources, and writing the final manuscript. Revisions were conducted by N.E. Hussey.

The unpublished manuscripts presented in Chapters 4 and 5 were co-authored by J.E. Edwards, K.J. Hedges, A.T. Fisk, and N.E. Hussey. In both cases, the author was responsible for providing the main ideas, data analysis and figure creation, interpretation, and writing the final manuscripts. Co-author contributions related primarily to the original experimental design and theoretical knowledge input, as well as hands-on contributions in the field components of the research. Additional guidance was provided by N.E. Hussey pertaining to the refinement of the study design and data analyses, as well as revision of all written contributions.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

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II. Declaration of Previous Publication

This thesis includes two original papers that have been previously published/submitted for publication in peer reviewed journals, as follows:

Chapter 2: Edwards, J.E., Hiltz, E., Broell, F., Bushnell, P.G., Campana, S.E., Christiansen, J.S., Devine, B.M., Gallant, J.J., Hedges, K.J., MacNeil, M.A., McMeans, B.C., Nielsen, J., Præbel, K., Skomal, G.B., Steffensen, J.F., Walter, R.P., Watanabe, Y.Y., VanderZwaag, D.L., and Hussey, N.E. (2019). Advancing research for the management of long-lived species: A case study on the Greenland shark. Frontiers in Marine Science. DOI: 10.3389/fmars.2019.00087. (*Published*)

Chapter 3: Edwards, J.E., Pratt J., Tress, N., and Hussey, N.E. (2019). Thinking deeper: Uncovering the mysteries of animal movement in the deep sea. Deep-Sea Research Part I: Oceanographic Research Papers. DOI: 10.1016/j.dsr.2019.02.006. (*Published*)

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ABSTRACT

Arctic ecosystems are highly seasonally dynamic, and as such, mobile Arctic species have adopted movement patterns that correspond to the occurrence of productivity hotspots. As polar regions continue to warm at an unprecedented rate, the predictable occurrence of these hotspots of may be reduced, resulting in dire consequences for long-lived or slow-adapting species. Effective marine management approaches will therefore rely on an understanding of the ability of Arctic predators to confer community stability by linking disparate food webs and by responding flexibly to environmental change. This thesis describes the use of static acoustic telemetry to examine the long-term movement patterns of a model mobile predator, the Greenland shark (*Somniosus microcephalus*) within two distinct habitat types (coastal and offshore waters) and across multiple years (7 y). Movement records for 155 tagged Greenland sharks revealed strong seasonality in coastal and offshore residency driven by fluctuations in sea-ice cover, with evidence of site fidelity to specific sites (receivers) in both regions. Juvenile sharks remained in coastal regions for longer durations than subadults, however, no size-based spatial segregation was observed. At a localized scale, sharks used deep-water channels to direct movements between a coastal fjord system and offshore waters, where they exhibited transient behaviour near offshore moorings located outside of identified hotspot regions. Ultimately, this research provides novel insight into the long-term movement dynamics of this potentially vulnerable Arctic predator and will inform future management practices that promote the longevity of this species.

DEDICATION

For their endless love, encouragement, and belief in my abilities, I dedicate this thesis to my parents, Vaughn and Mary Lee Edwards.

Thank you for fostering in me a deep devotion to the sea and an undying curiosity in the alien world that lies within it.

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together, sharing each other's company and the custody of many fish. Finally, to Laurissa, my first roommate and birthday twin, I will always cherish the moments we shared, in good times and bad, and the enduring kindness you have shown me.

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CHAPTER 1

General Introduction

The objective of this thesis is to define the movement behaviours and habitat use of a highly understudied top predator, the Greenland shark (*Somniosus microcephalus*), in the coastal and offshore marine ecosystems of the Canadian Arctic. This introductory chapter will provide background information on the study of movement ecology and its application for conservation and management, as well as considerations related to the current study system (deep-water and Arctic environments – specifically, Baffin Bay), the study species (the Greenland shark), and the rationale of my research. Subsequent chapters will cover a range of topics focused on improving our understanding of the movement behaviours of Greenland sharks in Arctic marine ecosystems and the application of movement ecology for the management of long-lived and inherently vulnerable deep-water species.

1.1 Movement ecology

Movement is an essential characteristic that unites living organisms and drives the ecological and evolutionary processes that shape plant and animal communities and the landscapes they inhabit (Dingle, 2014; Nathan et al., 2008). The study of movement ecology thereby strives to describe and understand the causes, patterns, and mechanisms by which organisms move throughout their environment, as well as the myriad consequences that occur as a result (Morales et al., 2010). Based on a movement ecology paradigm created to unify research in this field, organismal movement can be broken down into four basic components that drive specific patterns in movement paths and are, in turn, influenced by feedback mechanisms relating to the movement itself (Nathan et al., 2008):

The first factor is known as the internal state. This addresses the question of *why* organisms move and encompasses factors that influence the maintenance of physiological (and potential psychological) homeostasis, as well as drivers of evolutionary success such as the need to survive and reproduce. Second, movement patterns are strongly influenced by an organism's capacity for movement (*i.e.,* how to move), specifically referring to the mechanical methods used by an organism to self-propel or to be moved passively by external forces. An organism's navigational capacity then comes into effect, wherein individuals may use external cues to direct the timing or direction of movement to facilitate the achievement of biological goals. Finally, external elements, such as environmental or biological stimuli, may also affect movement via impacts on any of the three aforementioned factors.

These four components can be used separately or in concert to inform an enormous variety of movement-related questions (Hays et al., 2016; Lennox et al., 2019). For instance, recent studies have highlighted the application of movement ecology for wildlife conservation and management planning (Barrett, Buxton, & Gardner, 2009; Field, Meekan, Speed, White, & Bradshaw, 2011; Hobday, Hartog, Timmiss, & Fielding, 2010; Schrank & Rahel, 2004). This approach, which can incorporate information including a species' movement attributes, ecosystem impacts, and the scale of management required, can be applied to inform management decisions across a wide range of taxa and ecosystem types (Allen & Singh, 2016; Lascelles et al., 2014). The advancement of animal-borne telemetry technologies has played a critical role in this growing area of research by facilitating the acquisition of physiological (Metcalfe, le Quesne, Cheung, & Righton, 2012), geospatial (Southall et al., 2005), and environmental (Kristensen, Righton, Del Villar-Guerra, Baktoft, & Aarestrup, 2018) data *in situ*, thereby improving our understanding of how and why animals move and allowing us to address a variety of management concerns (Brooks et al., 2019).

1.2 Aquatic telemetry

Throughout history, the study of animal movement in the wild has been impeded by researchers' abilities to monitor the activities of their study subjects while minimizing their own influence on the behaviours they observe. In terrestrial ecosystems, visual observation approaches (*e.g.,* aerial or long-range photography/videography, autonomous remote photography/camera traps; [Cutler & Swann, 1999], remote sensing technologies; [Chen & Zhang, 2019]), and animal-borne tracking technologies (Ropert-Coudert & Wilson, 2005) have been in use for decades and are currently well established. In contrast, the development of such approaches for research on aquatic organisms has faced numerous challenges, including the vast scale and remoteness of open-water systems and the physical properties of aquatic environments that limit the deployment of electronic devices. Despite these challenges, several methods of remote observation have been developed for use in aquatic environments, ranging from baited cameras (BRUVs; Letessier, Bouchet, Reisser, & Meeuwig, 2015; Wheeland & Devine, 2018), to numerous forms of animal-borne technologies including cameras and telemetry devices such as accelerometers (Hays, 2015), archival data loggers (De Pontual et al., 2019), satellite tags (Heupel et al., 2015), and acoustic transmitters (Hussey et al., 2015; Lea, Humphries, von Brandis, Clarke, & Sims, 2016). To date, researchers and device manufacturers have prioritized the study of shallow-water or surface-associated animals, facilitating the use of light-based (Teo et al., 2004) and satellite geolocation (Bruce, Stevens, & Malcolm, 2006), and device recapture (*i.e.*, animal-borne tags and static receivers). However, the inability to send satellite signals through water, in addition to oceanographic factors corresponding to increases in depth, such as light attenuation, decreased temperature, and increased pressure, have greatly limited the advancement of telemetry technologies that are appropriate for use on deep-water species. As a result, only a handful of studies have examined animal movement in the deep sea (Edwards, Pratt, Tress, & Hussey, 2019), through the use of either satellite (Davidson & Hussey, 2019), archival (Boje, Neuenfeldt, Sparrevohn, Eigaard, & Behrens, 2014), or acoustic telemetry (Barkley, Hussey, Fisk, Hedges, & Treble, 2018; Hussey et al., 2017).

1.3 Animal movement in the deep sea

The deep sea, defined as all depths below 200 m, is a vast and understudied environment, comprising approximately 90% of the total area of Earth's oceans, and harboring some of the last unexplored habitats on the planet (Gage & Tyler, 1991; Ramirez-Llodra et al., 2010). To survive in this environment, deep-water species have evolved unique adaptations to overcome challenging conditions such as extreme pressures, low temperatures and light levels, and limited nutrient availability (Ramirez-Llodra et al., 2010). These harsh conditions have thereby shaped the life history strategies and behaviours of deep-water species, guiding the evolution of *K*-selected traits such as low metabolic rates, late age at maturity, low fecundity, and long lifespans (Norse et al., 2012; Simpfendorfer & Kyne, 2009). Scarce and infrequently occurring nutrient deposits have also led to a variety of adaptations to improve the detection and acquisition of food sources by deep-water organisms. These include enhanced chemoreception and mobility, which facilitate active search strategies and allow animals to locate and move between distant resource patches (Armstrong, Foley, Tinch, & van den Hove, 2012; Premke, Muyakshin, Klages, & Wegner, 2003).

1.3.1 Deep-water telemetry studies to date

Despite increasing interest in deep-sea environments for fisheries expansion (Norse et al., 2012) and natural resource extraction (Benn et al., 2010), very few studies have determined the geographic ranges of deep-water species, and even fewer have focused on describing their fine-scale movements. Successful studies have relied on custom-built devices (Bagley & Priede, 1997; Hissmann, Fricke, & Schauer, 2000) or the limited technologies available for use in the deep-sea (Brown, Brickle, & Scott, 2013), each presenting their own applications and constraints. For instance, archival data loggers can be deployed at great depths (maximum recorded depth of 1000 m; Boje et al., 2014) where they can collect high resolution environmental and physiological data over long durations (~3 y; Loher, 2011), however, these tags must be recaptured to obtain the archived data and geolocation estimates can typically only be produced using retroactive modelling approaches (Pedersen, Righton, Thygesen, Andersen, & Madsen, 2008). Satellite tags can also archive high resolution data such as depth and temperature and can remain active up to maximum depth of 1800 m (Brown et al., 2013), however, the need for a flotation device to bring the tag to the surface increases tag burden and, consequently, the minimum size of individuals suitable for tagging (Loher & Seitz, 2006). Furthermore, when deployed on deep-water animals that rarely (if ever) break the water's surface, satellite tags provide only straight-line trajectories estimated using the location of the tagged animal's release and the first reliable geolocation estimate upon the tag's release from the animal and transmission to ARGOS satellites (Campana, Fisk, & Peter Klimley, 2015; Edwards et al., 2019b). Finally, acoustic telemetry devices can remain active for extremely long durations (transmitters up to 10 y and receivers >1 y), however, commercially available acoustic receivers are currently only rated to a maximum depth of 500 m (VEMCO product specifications, https://vemco.com). Despite this limitation, some studies have successfully used commercial acoustic telemetry devices at depths beyond this rating, providing some of the first long-term movement datasets for deep-water species (Barkley et al., 2018; Daley, Williams, Green, Barker, & Brodie, 2015; Hussey et al., 2017).

1.4 Arctic marine ecosystems

The Arctic Ocean encompasses marine regions lying north of the Arctic circle (66°32'N) and is primarily defined by the presence of floating sea-ice which varies considerably in depth and extent, both interannually and across seasons (Serreze, Holland, & Stroeve, 2007). Arctic marine environments are also characterized by strong oceanographic variability produced by extreme seasonality in the intensity and duration (*i.e.*, daylight hours) of solar radiation (Gradinger, 1995; Walsh, 2008). Together, these seasonal shifts result in acute spatial and temporal variation in pelagic and ice-associated primary productivity and, in turn, the distribution of available resources (Tremblay et al., 2012).

Harsh environmental conditions that limit primary productivity in Arctic ecosystems also limit the distribution and abundance of biological communities which, similar to deep-water ecosystems, are generally composed of late-maturing, long-lived species (Barrie et al., 1992). Arctic communities possess low species diversity, and were therefore historically considered to have relatively short food chains with simplified predator-prey relationships (Barrie et al., 1992). More recent studies, however, suggest that Arctic food webs are composed of complex feeding interactions (Wirta et al., 2015) wherein upper trophic level consumers (large, mobile predators in particular) confer community stability by coupling energy pathways derived from disparate sources of primary production (McCann, Rasmussen, & Umbanhowar, 2005; McMeans, Rooney, Arts, & Fisk, 2013). Specifically, in expansive and spatially diverse ecosystems (such as the Arctic marine realm), mobile predators operate at larger spatial scales than their prey, allowing them to demonstrate rapid behavioural flexibility by choosing between distinct resource patches and, consequently, to dampen oscillations in lower tropic levels (McCann et al., 2005; McCann & Rooney, 2009). For example, in Baffin Bay (a deep-water ocean basin bordered by eastern Canada and west Greenland) many large-bodied, Arctic species have adapted to seasonal variability in ice-cover and productivity by developing transient movement strategies that correspond to the occurrence of broadly-distributed resource patches (see *Chapter 5: Introduction* for further detail) (Barkley et al., 2018; Dueck, Hiede-Jørgensen, Jensen, & Postma, 2007; Laidre et al., 2004; Marcoux, Ferguson, Roy, Bedard, & Simard, 2017).

1.4.1 Climate change and threats to Arctic marine environments

In recent decades, the Arctic has been warming at nearly twice the global average rate, with mean annual temperatures increasing by ~2-3 ºC and winter temperatures increasing by up to 4 ºC since the 1950s (ACIA, 2005; Graversen, Mauritsen, Tjernström, Källén, & Svensson, 2008; Rigor, Colony, & Martin, 2000). Changes in atmospheric heat transport and feedback mechanisms resulting from the loss of reflective snow and ice cover (and the subsequent increase in the absorption of solar radiation by Artic seas and landmasses) have been suggested as potential drivers of this excessive warming - an anomaly which is often referred to as the “Arctic amplification” (ACIA, 2005; Graversen et al., 2008; Serreze et al., 2007).

By shifting the physical characteristics of Arctic environments, climate-induced changes have already begun to vastly impact the lives of Arctic flora, fauna, and human residents alike (West, 2009). In the marine realm, warming ocean temperatures and sea ice reductions have been shown to coincide with the northward range expansion of temperate species, leading to the borealization of polar fish communities (Fossheim et al., 2015). Simultaneously, fish species with affinities to cold temperatures have been shown to retract their range northward and into deeper waters in response to higher bottom temperatures with implications for both commercial fisheries and marine management (Dulvy et al., 2008; Perry, Low, Ellis, & Reynolds, 2005). Changes in sea ice extent have also caused dramatic shifts in the distribution of apex consumers such as the killer whale (Higdon & Ferguson, 2009), and have influenced the movement patterns, distribution, and reproductive success of native Arctic predators, many of which are highly dependent on ice-derived food chains and/or use sea ice for behaviours such as resting, foraging, and rearing young (Tynan & Demaster, 2016; Wassmann, Duarte, Agustí, & Sejr, 2011). Due to their importance for providing stability to marine food webs, declines in the abundance of apex predators could have cascading top-down effects on the community structure, function, and vulnerability of Arctic marine ecosystems (Fossheim et al., 2015; McCann, Rasmussen, & Umbanhowar, 2005; Smetacek & Nicol, 2005).

Under projected warming scenarios, mechanisms of bottom-up control may also cause dramatic changes to community structure in Arctic marine ecosystems. Given current rates of warming and loss of sea-ice, Arctic ecosystems are likely to cross an ecological tipping point resulting in a transition from diatom-dominated planktonic communities (which act as a CO_2 sink) to picoplankton-dominated communities (acting as a CO_2 source), altering carbon transfer and food web production and causing a cascade of ecosystem-wide effects that will likely be irreversible (Duarte et al., 2012; MacNeil et al., 2012; Wassmann et al., 2011). A predicted consequence of this shift is that the loss of nutrient transfer from sea-ice associated planktonic communities to the benthos will negatively impact Artic fish species, many of which are demersal and are adapted to exploit a relatively narrow range of food sources (Fossheim et al., 2015). This dietary specialization (and resulting vulnerability to climate change), compounded by the loss of suitable habitat and competition with an increasing number of boreal species, will likely pave the way for the further success of temperate invaders (Fossheim et al., 2015).

Furthermore, without the restrictions posed by hostile temperatures and sea ice, human activities such as shipping, fishing, natural resource extraction, tourism, infrastructure development, and military exercises will extend their reach northward alongside the movements of migrating temperate species (Duarte et al., 2012; Pechsiri, Sattari, Martinez, & Xuan, 2010). This increase in human presence in the Arctic, leading to more frequent interactions between humans and wildlife, the modification of terrestrial and marine habitats, and heightened exploitation rates, will have unprecedented consequences for Arctic ecosystems (Duarte et al., 2012; Huntington et al., 2007; Pechsiri et al., 2010).

Despite these growing threats and the dramatic rate of Arctic warming, limited research has focused on assessing the current and predicted consequences of climate change (Wassmann et al., 2011). Moreover, very few studies have described the baseline conditions present in polar ecosystems which are known to house a disproportionate number of understudied species relative to low latitude environments (Christiansen, Mecklenburg, & Karamushko, 2014; Dey, Yurkowski, Schuster, Shiffman, & Bittick, 2018). This lack of information is of particular concern given the fact that many Arctic species possess life history traits that make them vulnerable to overexploitation (*e.g.,* low fecundity, long lifespans, etc.) and may be limited in their capacity to adapt rapidly to environmental changes using behavioural or demographic responses (Dulvy, Sadovy, & Reynolds, 2003; Perry et al., 2005). The low species diversity in Arctic ecosystems also confers limited functional redundancy to polar food chains, making the loss of a single species potentially catastrophic to those species that depend upon it for survival (Pechsiri et al., 2010). Given the current rate of warming and future climate projections, studies that address data disparities in both of these areas will be essential for the preservation of Arctic biodiversity.

1.4.2 Baffin Bay

Baffin Bay is a large, semi-enclosed ocean basin situated between Baffin Island (Nunavut, Canada) and Northwestern Greenland with a maximum depth of approximately 2000 m. To the south, the bay is linked to the North Atlantic by a deep-water sill (640 m) in the Davis Strait, and in the north, it connects to the Arctic Ocean via shallower sills located in Lancaster Sound (125 m depth), Jones Sound (190 m depth), and Nares Strait (220 m depth) (Münchow, Falkner, & Melling, 2015). Along its continental margins, Baffin Bay is ringed by wide, sloping shelf areas off Greenland, and more steeply sloping shelves off Baffin Island, both of which are broken by a series of deep channels (~500 – 1000 m depth) connecting offshore waters to its coastal fjords (Münchow et al., 2015).

Circulation patterns in Baffin Bay are driven by two major North Atlantic current systems known as the West Greenland and Baffin Island Currents. Warm and salty water ($T > 0^{\circ}C$, $S > 34$) from the North Atlantic enters the bay from the south through the eastern Davis Strait, moving northward along the west coast of Greenland, where it is met by inflows of Arctic water from the Smith, Lancaster, and Jones Sounds (Tang et al., 2004). Following this cyclonic flow, the Baffin Island Current then moves southward down the eastern coast of Baffin Island, resulting in a prominent outflow through western Davis Strait (Tang et al., 2004). These currents are subject to interannual forcing by trends in the North Atlantic Oscillation (NAO), where NAO-positive years are associated with fresher, colder surface waters off Baffin Island, saltier, warmer waters off Greenland, and an energetic increase in circulation throughout Baffin Bay (Münchow et al., 2015).

Baffin Bay is also characterized by seasonal, semi-complete coverage of sea-ice, with formation beginning in October, increasing in a southerly direction and reaching near-complete coverage in March (Tang et al., 2004). Predominantly ice-free periods occur only in August and September (Tang et al., 2004), however, a recurrent patch of open water known as the North Water (NOW) Polynya can typically found be spanning the region between Smith and Lancaster Sounds (~76˚N to 79˚N and 70˚W to 80˚W) throughout the ice-covered months (Heide-jørgensen et al., 2013). The NOW is characterized by enhanced atmospheric heat loss and increased formation of sea-ice which is then carried away from the region by persistent north winds and southerly currents, leading to its designation as a 'latent heat' polynya (Melling et al., 2001; Tang et al., 2004). The existence of this polynya is also accredited to the formation of an ice bridge in Smith Sound which prevents ice from entering the bay from the north (Dumont, Gratton, & Arbetter, 2009). In Arctic ecosystems, polynyas such as this are considered to be hotpots of primary productivity due to significant upwelling and reduced ice cover allowing more sunlight to reach surface waters, as well as aggregation sites for numerous marine mammals and birds (Heide-jørgensen et al., 2013; Melling et al., 2001).

1.5 The Greenland shark

The Greenland shark (*Somniosus microcephalus*) is a member of the family Somniosidae - commonly referred to as the 'sleeper sharks' due to their slow swim speeds and perceived low activity levels - and is the only shark species to inhabit the periodically ice-covered regions of the North Atlantic and adjacent Arctic waters (MacNeil et al., 2012). Due to its high trophic position (4.8) (Fisk, Tittlemier, Pranschke, & Norstrom, 2002), large body size (up to ~550 cm total length; Campana et al., 2015; Nielsen, Hedeholm, Simon, & Steffensen, 2014), and movement capacity (Campana et al., 2015; Fisk, Lydersen, & Kovacs, 2012; Hussey et al., 2018), this species is thought to play a key role in providing ecosystem stability throughout the waters of Baffin Bay by linking coastal and offshore food webs (McMeans, Arts, et al., 2013; McMeans, Rooney, et al., 2013).

1.5.1 Biology and behaviour

Recently designated the world's longest-lived vertebrate (Nielsen et al., 2016), the Greenland shark is thought to possess other *K*-selected life history traits such as low fecundity and slow growth (0.5 cm yr^{-1}; Hansen, 1963), potentially as a result of extremely slow metabolic rates (Ste Marie et al. unpublished). Traits such as these are typically thought to infer an increased vulnerability to exploitation (Koslow et al., 2000; Simpfendorfer & Kyne, 2009), prompting concern over the conservation of this species (Davis et al., 2013; Edwards et al., 2019b). Notably, Greenland sharks also exhibit the slowest observed mean swim speed (0.34 ms^{-1}) and tailbeat frequency (0.15 Hz) relative to their size for any fish species (Watanabe, Lydersen, Fisk, & Kovacs, 2012). Nevertheless, Greenland sharks are capable of traveling vast distances, as recorded by satellite telemetry devices deployed on free-ranging individuals (Campana et al., 2015; Fisk et al., 2012; Hussey et al., 2018). As such, Greenland sharks have a broad distribution throughout the deep-water coastal and offshore regions of Baffin Bay, and are thought to have the potential to range globally where deep-water temperatures remain below 5˚C (MacNeil et al., 2012). Telemetry studies have also revealed a tendency for Greenland sharks to move vertically throughout the water column (Gallant, Rodriguez, Stokesbury, & Harvey-Clark, 2016; Skomal & Benz, 2004; Stokesbury, Harvey-Clark, Gallant, Block, & Myers, 2005), with visual sightings (Borodavkina, Chernova, & Chekmeneva, 2019; Idrobo & Berkes, 2012) and telemetry records placing sharks in surface waters down to a maximum recorded depth of 1,816 m (Campana et al., 2015).

1.5.2 Diet

The Greenland shark's diet consists of a variety of invertebrates, marine mammals, and both pelagic and demersal teleost fishes, including gadoids and one of the Arctic's few commercially harvested species, the Greenland halibut (*Reinhardtius hippoglossoides*) (Fisk et al., 2002; L. M. E. Leclerc et al., 2012; McMeans, Svavarsson, Dennard, & Fisk, 2010). The importance of benthic fish species in the Greenland shark's diet suggests that they may be dependent on ice-associated primary production and could be heavily impacted by the loss of sea ice and resulting changes to the structure of deep-water food webs (MacNeil et al., 2012). In spite of its remarkably slow swim speeds, dietary studies also show evidence of both scavenging and live prey capture by Greenland sharks, resulting in uncertainty among researchers regarding the shark's true predatory capabilities (Edwards et al., 2019b; MacNeil et al., 2012; McMeans et al., 2010). While several cases of marine mammal tissue, and even whole animals (typically juvenile seals), found in Greenland shark stomachs have been reported (Fisk et al., 2002; L. M. Leclerc et al., 2011; McMeans et al., 2010), the exact mechanism used by the sharks to feed on fast-moving prey is the topic of continued debate (Edwards et al., 2019b; Watanabe et al., 2012). Confirmation of the Greenland shark's ability to predate on live marine mammals would lend further support to its theorized role as an apex predator that can exert top-down control in Arctic marine ecosystems, making such evidence invaluable (MacNeil et al., 2012).

1.5.3 Threats

Despite being the largest fish to inhabit Arctic waters, Greenland sharks face a growing number of threats to individual survival and population resilience (*see Section*

2.10: Threats to Greenland shark populations; Edwards et al., 2019b). Until the mid-20th century, fisheries operating out of Greenland, Iceland, and Norway harvested a combined total of approximately 50,000 Greenland sharks each year to produce lamp oil from the animals' large and fatty livers (MacNeil et al., 2012). A decline in demand eventually prompted the closure of these targeted fisheries, however, the capture of Greenland sharks by commercial Arctic fisheries continues at a much lower levels today (Davis et al., 2013; Edwards et al., 2019b). In addition to small-scale modern fisheries operating out of Iceland and Greenland, Northern Canadian fisheries targeting Greenland halibut and northern shrimp (*Pandalus borealis*) reported incidental captures of ~5.5 tons per year between 1996 and 2015 (Department of Fisheries, and Oceans [DFO], 2016). Furthermore, while bycaught Greenland sharks must be returned to the water immediately following capture, many are reported dead prior to release, with post-release mortality rates varying by gear type and set duration (Bryk, Hedges, & Treble, 2018; NAFO 2018). Given expected increases in fishing pressure in the coming years (Christiansen et al., 2014), in addition to impending threats posed by more frequent seismic surveys, increased vessel traffic, and pollution, the management of Greenland sharks is of growing concern for researchers and fisheries managers at both federal (DFO; Treble & Stewart, 2010) and intergovernmental scales (Northwest Atlantic Fisheries Organization; NAFO 2017) (Edwards et al., 2019b).

1.5.4 Data deficiencies and conservation concerns

While bycatch records from commercial and Inuit fisheries indicate an apparent abundance of Greenland sharks in waters throughout Baffin Bay (NAFO 2018), research on this species has thus far been limited. This disparity can be largely attributed to the financial and logistical challenges associated with conducting research in extreme Arctic conditions (Mallory et al., 2018) and the inaccessibility of polar study sites throughout much of the year (Dey et al., 2018). As a result, many questions regarding aspects of Greenland shark biology (*e.g.,* reproduction, metabolism), behaviour (*e.g.,* movement patterns, predatory capabilities) and its ecological role remain unanswered (Edwards et al., 2019b). Furthermore, the species is minimally represented in traditional Inuit knowledge, predominantly due to their lack of cultural or nutritional significance to the Inuit of Baffin Island and to the low rate of interactions between Inuit and Greenland sharks prior to the onset of community longline fisheries in the region (Idrobo, 2008; Idrobo & Berkes, 2012). Together, the lack of fundamental biological and ecological information for the Greenland shark, and its nominal cultural and commercial importance, have greatly impeded efforts to develop effective management strategies for this species thus far (Davis et al., 2013). There is therefore a pressing need for further studies to facilitate the management of this potentially vulnerable species while simultaneously improving our understanding of the role of apex predators in Arctic marine ecosystems.

1.6 Rationale and objectives

As Arctic ecosystems become increasingly vulnerable to the effects of anthropogenic and climate-induced stressors, an understanding of the energetic pathways that confer community stability is critical to avoid ecosystem collapse (McMeans, Rooney, et al., 2013). In highly seasonal environments such as the Arctic, mobile consumers that forage across a variety of landscapes (*e.g.,* coastal *vs.* pelagic environments) can maintain food web stability by coupling disparate energy pathways and exhibiting behavioural flexibility in response to changing resource conditions (McCann et al., 2005; McMeans, Rooney, et al., 2013). In the Eastern Canadian Arctic, its high trophic position and capacity for broad-scale movements make the Greenland shark (*Somniosus microcephalus*) an excellent model predator for examining ecosystem connectivity over a range of spatial and temporal scales. Static acoustic telemetry provides one approach to improve our understanding of Greenland shark movements, migratory patterns, and spatial habitat use in Arctic marine ecosystems.

The purpose of this thesis can be broken down into three overarching goals that establish the basis for the two literature reviews and two data chapters included herein. The first review chapter (presented in *Chapter 2*) aims to draw from the current literature and expert advice to evaluate research priorities and methodologies that are essential for developing a management strategy for the Greenland shark. These findings will direct the goals of subsequent data chapters as well as future research conducted by members of the broader scientific community. Second, I will provide a detailed assessment of the challenges, available technologies and methodologies, and study findings reported by all telemetry studies conducted in the deep-sea to date (*Chapter 3*). The goal of this chapter is to identify the potential applications of various telemetry techniques for examining the movement ecology of deep-water species and to promote the importance of collecting baseline data for deep-sea communities given current and predicted rates of exploitation. Finally, my two data chapters will examine the behaviour of a highly understudied and potentially vulnerable Arctic predator, the Greenland shark, using static acoustic telemetry. Examination of archived movement data will be used to determine how distribution, residency, and movement behaviours differ across an ecosystem exhibiting marked spatial and seasonal variability. Specifically, the seasonal and interannual movement patterns of tagged Greenland sharks will be quantified at two spatial scales (localized and basin-scale) and in two marine habitat types (a coastal fjord and offshore waters) in Baffin Bay (Eastern Canadian Arctic). Data pertaining to each of these paired habitats and spatial scales (fine-scale coastal movements, and large-scale offshore movements) will form the basis for *Chapters 4* and *5* of this thesis, respectively.

Chapter 4 will focus on the temporal patterns of coastal residency (*e.g.,* timing and duration), inshore-offshore connectivity, and habitat use (*e.g.,* core and general home ranges) exhibited by tagged sharks detected in Scott Inlet and Sam Ford fjord within and across multiple years. For sharks that return to the fjord in subsequent years following tagging, individual movement behaviours will be compared between the tagging year and subsequent detection years to identify potential post-release behavioural modifications. In addition, the behavioural responses of tagged Greenland sharks (*i.e.,* presence or absence in the fjord system) will be compared to seasonal and inter-annual changes in environmental conditions such as sea-ice cover, temperature at depth, and lunar cycle to determine the drivers of residency in coastal waters.

Analyses conducted in *Chapter 5* will assess the timing and distribution of Greenland shark movements in the offshore regions of Baffin Bay, highlighting connectivity between coastal and offshore habitats, evidence of site fidelity, and hotspots of occurrence in offshore waters. Multiple years of detections archived by four coastal and three offshore receiver arrays will be used to examine seasonality in the use of these two marine habitat types by tagged Greenland sharks.

I hypothesize that the Greenland shark’s long lifespan, high degree of mobility, and opportunistic foraging strategy will drive individuals to adopt temporally fluctuating patterns of distribution, residency, and movement path structure that correspond to the seasonal availability of resources throughout the study system. Specifically, sharks are expected to be concentrated in coastal fjords during periods of peak inshore productivity (spring and summer) where they will demonstrate a high degree of residency. In the less productive winter months, sharks will be more widely dispersed throughout the ice-covered ocean basin, exhibiting a lower degree of residency near offshore receivers and predominantly transitory movements. The long-term data available are unique to this study, providing novel insight into movement dynamics of this polar predator. These data will ultimately improve our ability to predict the influences of shifting climatic conditions and increased fishing pressure in Arctic regions on Greenland shark populations in the future.

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CHAPTER 2

Advancing research for the management of long-lived species: A case study on the Greenland shark

2.1 Introduction

The classification of life history traits along a continuum between *r*- and *K*-selection is regarded as a foundational tool for predicting the ability of animal populations to effectively respond to environmental and/or anthropogenic disturbance (Pianka, 1970). In higher order vertebrates, extreme longevity is commonly associated with the possession of *K*-selected life history traits that influence maximum intrinsic population growth rates (r_{max}) – such as slow growth, late maturity, and relatively low recruitment rates (McCann and Shuter, 1997). Such traits are thought to limit the ability of animal populations to sustain high levels of mortality (Adams, 1980; Musick, 1999a; Simpfendorfer and Kyne, 2009; Norse et al., 2012). In chondrichthyans, the frequency of these *K*-selected traits becomes more pronounced with increasing depth (Rigby and Simpfendorfer, 2015), resulting in significantly lower rates of population increase in deep-water species, and a heightened vulnerability to exploitation and incidental mortality relative to their shallow-water counterparts (García et al., 2008; Simpfendorfer and Kyne, 2009). Many deep-water species are currently targeted in commercial fisheries (Barker and Schluessel, 2005) and the number of deep-water habitats affected by fishing is expected to increase (Halpern et al., 2008). In addition, impacts from other human activities (*e.g.,* seismic surveys) on deep-sea biota are virtually unknown, as are the chronic and cumulative impacts from multiple stressors, including climate change and pollution. The importance of longevity in influencing the vulnerability of animal populations to overexploitation has long been overlooked in conservation and management planning. It is only relatively recently, following well-known examples of overfishing (*e.g.*, New Zealand orange roughly, *Hoplostethus atlanticus*, and North Atlantic cod, *Gadus morhua*; Walters and Maguire, 1996; Clark, 2001) and declines in many long-lived marine species (Myers and Worm, 2003; Heppell et al., 2005), that there has been increased consideration of *K*-selected traits in marine management policy (Musick, 1999b; Musick et al., 2000; Baum et al., 2003). This is especially true for the protection of species targeted by commercial or recreational fisheries, including some deep-water chondrichthyan and teleost fishes (Stevens et al., 2000; Simpfendorfer and Kyne, 2009; Norse et al., 2012; Rigby and Simpfendorfer, 2015). While current literature asserts the importance of longevity for predicting the effects of anthropogenic disturbance on wild populations, the mechanisms driving extreme longevity and its influences on animal behavior and population dynamics are not well understood. The Greenland shark (*Somniosus microcephalus*) is a newly recognized example of an extremely long-lived deep-water chondrichthyan (estimated lifespan of at least 272 years; Nielsen et al., 2016), that is both data deficient and vulnerable to human threats such as fishery-related mortality (Davis et al., 2013). Greenland sharks are primarily known to inhabit deep-water and coastal regions of the Arctic and North Atlantic (Yano et al., 2007, see Figure 1 for capture locations from the reviewed studies), but have the potential to range globally where deep-water temperatures are <5 °C (MacNeil et al., 2012) and have been observed both at the surface and at confirmed depths up to 1,816 m (Campana et al., 2015a, Somniosid spp. Have also been observed at 2,200 and 2,992 m; Herdendorf and Berra, 1995; Porteiro et al., 2017, respectively). While historically fished in the waters off Iceland, Greenland, and Norway to support a liver oil industry, decreased demand in the mid-20th century prompted the closure of targeted fisheries; currently, Greenland sharks are primarily caught as bycatch in commercial longline, gillnet, and bottom trawl fisheries (Davis et al., 2013). Despite a recent spike in public interest due to its reported longevity, logistical challenges continue to impede the detailed study of this species. Consequently, relatively little is known about several important aspects of Greenland shark physiology (*e.g.,* metabolism, reproduction), ecology (*e.g.,* age class structure, distribution, ecological role, genetic variability), and behavior (*e.g.,* predatory capabilities, horizontal movement patterns). The primary objective of this paper is to highlight important knowledge gaps that limit the development of a management framework for the Greenland shark. In the following text, we discuss a variety of forward-thinking experimental approaches that will enable researchers to answer key questions about Greenland shark biology and ecology (**Table 2.1**). Additionally, we present these current and future advances in Greenland shark research within the context of broader issues regarding the study of long-lived species (**Table 2.2**).

2.2 Methods

Experts in the study of Greenland sharks from several research and management institutions were consulted. Guided by the previous scientific contributions of this expert team, eight topics were deemed to be of high priority to assist future Greenland shark research and management. The chosen topics are outlined in the text as follows: (1) Demographics and life history, (2) Population genetics and genomics, (3) Movement ecology, (4) Behavior, (5) Physiological adaptations, (6) Diet and trophic ecology, (7) Threats to Greenland shark populations, and (8) Management (see **Figure 2.1** for study count by research topic). Each topic was then organized into four key sections: (i) current knowledge in the chosen field, (ii) identified knowledge gaps and limitations, (iii) proposed strategies to address identified data deficiencies, and finally, (iv) potential recommendations for Greenland shark management. While some topic overlap among sections was unavoidable due to the interconnected nature of much of the examined and proposed research, attempts were made to minimize this.

2.3 Demographics and Life History

Recent radiocarbon dating of Greenland shark eye lenses supports the long-standing prediction of exceptional longevity in this species (Nielsen et al., 2016; **Figure 2.2A**). These data also provide the first age-at-length data for Greenland sharks.

Current knowledge of Greenland shark distribution and population abundance are based on exploratory fisheries surveys, stock assessments of commercial species (*e.g.*, Greenland halibut, *Reinhardtius hippoglossoides*, and Northern shrimp, *Pandalus borealis*), and bycatch reports from commercial and historical fisheries. Contemporary catch is restricted to small-scale targeted fisheries in Greenland and Iceland, as well as incidental bycatch in a variety of North Atlantic and Arctic fisheries (ICES, 2017). In the Barents Sea, annual Greenland shark bycatch is estimated to be 140–150 tons (Rusyaev and Orlov, 2013) and in northern Canada, 105 tons between 1996 and 2015 (Department of Fisheries, and Oceans [DFO], 2016). However, annual bycatch is likely to be much higher, with an estimated bycatch of 1000 tons/y in the Uummannaq district in northwestern Greenland alone (Gunnarsdottir and Jørgensen, 2008; ICES, 2017).

Scientific catch data suggest regional differences in the relative abundance of Greenland sharks by life stage/size and sex. For example, no adult females [>4 m total length (L_T), Yano et al., 2007] have been reported throughout the Canadian Arctic and in Svalbard (Norway) despite intense sampling (N > 300 individuals, Skomal and Benz, 2004; Fisk et al., 2002, 2012; Leclerc et al., 2012; Hussey et al., 2015a, 2018; Devine et al., 2018). In contrast, adult females appear to be more frequent off southwestern Greenland, Iceland, and Newfoundland (Canada) (Yano et al., 2007; McMeans et al., 2010; Nielsen et al., 2014, 2016; Campana et al., 2015a), and several females > 5 m have been measured off Atlantic Canada (Campana personal communication). Juvenile sharks, defined as individuals ≤200 cm L_T, have been observed in both inshore and offshore waters (Hussey et al., 2015a), including animals within the birth size range (40–100 cm, MacNeil et al., 2012). Specifically, juveniles were observed in longline, trawl, and camera surveys within Scott Inlet, Baffin Island, and in offshore waters >1000 m depth (Fisk et al., 2002; Yano et al., 2007; Nielsen et al., 2014; Hussey et al., 2015a; Devine et al., 2018).

Baited remote underwater video (BRUV) surveys have provided the first estimates of the relative abundance of Greenland sharks in the Canadian Arctic (independent of bycatch data; Devine et al., 2018, **Figure 2.2C**). By identifying individuals using scar patterns and coloration, the number of sharks observed in each camera deployment was quantified, allowing estimations of observation rate across sampled regions (Devine et al., 2018, Figure 2D). BRUV surveys and exploratory fisheries in the Canadian Arctic Archipelago have also expanded the species' known northern and western ranges in inshore Canadian waters, highlighting the extent to which their range was historically defined by the spatial extent of commercial fisheries.

While radiocarbon dating of eye lenses has provided baseline age estimates for this species, these estimates still need to be verified with an independent, accurate, and precise age determination technique. However, the absence of hard tissues containing growth bands (such as fin spines, calcified vertebra, *etc.*) complicates such a validation. Other chemical dating techniques, such as aspartic acid racemization (which has been successfully applied on several cetaceans; George et al., 1999; Garde et al., 2007) have proven to be unsuccessful in providing independent age estimates for this species (Nielsen, 2013), highlighting the need for innovative aging methodologies.

In addition, many questions concerning population demographics – particularly population size and productivity, as well as reproductive biology, fertility, and natural mortality remain unknown or poorly understood. For example, knowledge of the reproductive biology of Greenland sharks is extremely limited. Only one pregnant female with ten near-term pups of 37 cm L_T has been reported (Koefoed, 1957). Observations of a high ovarian fecundity (>400 goose-egg sized unfertilized ova; Bjerkan, 1957; Yano et al., 2007; Nielsen et al., 2014; Campana personal communication) suggest that embryos may be aplacental viviparous, similar to those of spiny dogfish (*Squalus acanthias*) and Portuguese sharks (*Centroscymnus coelolepis*) (Campana et al., 2009; Castro, 2011). The gestation period, the locations of mating and pupping grounds, and the mating period all remain unknown. Greenland sharks may exhibit seasonal migrations for reproductive purposes (mating and pupping), but the existence or possible extent of connectivity between regions has yet to be documented. Given its extended longevity and the low productivity of sharks relative to teleosts (Musick, 1999a), the Greenland shark is expected to have particularly low productivity.

There is also a general lack of knowledge on the size and sex of Greenland sharks caught as bycatch in commercial fisheries (past and present) (Section “Threats to Greenland Shark Populations”, **Figure 2.2E**). Consequently, data available to evaluate the spatial distribution of shark life stages are sparse. Fishery-derived data are also problematic for estimating population abundance due to the spatially targeted nature of fisheries which limits the ability to extrapolate catch rates to larger areas. Estimation of the spatial distribution of Greenland sharks using commercial bycatch records is further confounded by misidentification with other large (but unrelated) shark species, for instance the basking shark (*Cetorhinus maximus*; Campana et al., 2008b).

Improved or novel age determination methods need to be developed for the routine aging of Greenland sharks (and sleeper sharks in general). With uncertainty surrounding age estimates for Greenland sharks, an improved understanding of the residence time and pathway of past bomb radiocarbon pulses into deep Arctic waters and in Greenland shark prey is required to improve the precision and accuracy of the radiocarbon dating method. Data are available for the otoliths of some Arctic fishes, beluga whale teeth, and vertebrae from several lamniform sharks (Stewart et al., 2006; Campana et al., 2008a; Hamady et al., 2014), but the organic pathway for the eye lens is not well-documented. Equally, mark-recapture methods could provide accurate estimates of size-dependent growth, which can be used to model growth rate (Francis, 1988), and thus age, with few assumptions. However, acquiring precise lengths for such large sharks at both tagging and recapture requires careful measurement in the field under logistically challenging conditions (as described by Hansen, 1963; see also **Figure 2.2B**) and a reliance on fishers to provide accurate length estimates for bycaught sharks.

The broad-scale use of BRUVs and modification of established population assessment methodologies should address many remaining questions about Greenland shark distribution and abundance (**Table 2.1**). Systematic surveys of local traditional knowledge and accounts from fishermen could help fill gaps in distribution, while the expansion of BRUV surveys could explore differences in relative abundances among sites, and seasonal BRUV surveys could help determine cyclic patterns in distribution. Although scar patterns and the coloration of individuals may change over time (Robbins and Fox, 2012), the use of colored Floy tags or other external markers could provide reliable long-term identification for both BRUVs and fishery-mediated surveys (**Table 2.2**). By modifying conventional mark-recapture models to integrate auxiliary data derived from acoustic or satellite telemetry, the effects of low recapture rates can be offset, resulting in more precise estimates of demographic parameters such as apparent survival and abundance (Dudgeon et al., 2015).

More data are needed to evaluate variation in life stage distribution patterns among regions. Such data can be collected from sharks caught in commercial fisheries as bycatch (*e.g.*, improving data collection on capture location, L_T, and sex; see **Table 2.1**), as well as by expanding large-scale, long-term tagging studies to include all life stages (see section "Movement Ecology"). Detailed reporting of Greenland shark bycatch will also improve growth rate estimates, as well as our understanding of exploitation rates and migration pathways, and could highlight sensitive areas for specific life stages. Tagging and release of mature females with pop-up archival satellite tags (during the open water season) could help identify critical habitats or areas that are important for mating and/or pupping, while at-sea sampling of bycatch mortalities will provide opportunities for the biological examination of mature or maturing females and additional data on ovarian and uterine fecundity.

Biological reference points and conservation targets typically require either population productivity values (based on growth and reproduction) or stock-recruitment curves (based on spawning stock biomass and fecundity). In the absence of these data for Greenland sharks, precautionary measures will be needed to protect sensitive habitats (such as potential mating grounds, pupping grounds, and nursery areas) and limit total catch. Identification of these ecologically important habitats is therefore critical for mitigating bycatch (see section “Movement Ecology”). Another key difficulty in setting conservation limits is uncertainty over whether historical catch rates of around 50,000 individuals/y in the northern European liver oil fishery (MacNeil et al., 2012) were sustained by local populations or emigration from a wider meta-population. Given the importance of these population-level data for implementing precautionary measures, assessments of current Greenland shark abundance and distribution should be made a high priority (**Table 2.1**).

2.4 Population Genetics and Genomics

Molecular genetic data, primarily based on mitochondrial DNA (mtDNA), has yielded important insight into the phylogeographic evolutionary history of the Greenland shark and other members of the genus *Somniosus*. Early work focused on the Pacific sleeper shark (*S. pacificus*), but also included a number of Greenland sharks and revealed relatively shallow genetic divergence between these two species (~1.8% sequence divergence; Murray et al., 2008). This study also documented the first evidence of haplotype sharing between two recognized *Somniosus* species (*S. pacificus* and the southern sleeper shark, *S. antarcticus*; Murray et al., 2008), contrasting the earlier resurrection of *S. antarcticus* as a distinct species (Yano et al. 2004). Further evidence of interspecies haplotype sharing has been reported for several juvenile Greenland sharks from the high Arctic that were found to be carrying *S. pacificus* mtDN haplotypes (Hussey et al., 2015a). More recently, a full mtDNA genome sequenced with phylogenetic reconstruction placed the Greenland shark and Pacific sleeper shark as sister species with respect to other major shark orders (Santaquiteria et al., 2017). By calibrating the mitogenomic phylogenetic reconstruction with fossil records and geological events, the speciation time of these two species was confirmed to be 3.5 million years ago (mya) (Santaquiteria, 2016; in agreement with Murray et al., 2008). A further phylogeographic study also confirmed mtDNA haplotype sharing between Greenland and Pacific sleeper sharks at additional locations as well as nuclear admixture, implicating interspecific hybridization as a phenomenon among Atlantic Somniosids (Walter et al., 2017). These data yielded a more recent speciation time for Greenland sharks than findings obtained using whole mitogenomes (2.1 mya versus 3.5 mya). Reconciling the rates of intra- and inter-specific admixture among the Somniosids with (incipient) speciation therefore holds much promise for clarifying the phylogeographic evolutionary history of this genus.

Reliance on mtDNA data to date paints an incomplete picture of the evolutionary history of the Greenland shark. Shared genetic signatures among extant species have led researchers to question the validity of current species descriptions, suggesting that a more comprehensive systematic revision of the genus is needed. In addition to signals of interspecific gene flow and incipient speciation, the demographic history of the

Greenland shark across its range indicates that the Atlantic population has persisted at a low, but stable size over the last 5 million years. This was likely followed by a recent population increase around 500,000 years ago, possibly linked to fluctuations in Arctic sea ice conditions during the Pleistocene. As yet, no clear or conspicuous regional geographic structure has emerged from the mtDNA data, aside from indications of genetic admixture (Murray et al., 2008; Walter et al., 2017).

The potential for extreme longevity exhibited by Greenland sharks (Nielsen et al., 2016) presents unique challenges for estimating relevant conservation parameters such as effective population size (N_e) (**Table 2.2**). Firstly, the value of N_e is highly sensitive to generation time. While estimates of N_e (both long-term and short-term estimates) are possible from genetic data, the translation of these values to biologically relevant terms is not straightforward. For example, coalescent-based estimates of long-term N_e were obtained from a 702 bp fragment of Cytochrome b using 20 and 150 y generation times (Walter et al., 2017), the latter based on an estimated age at first reproduction of 156 ± 22 years (Nielsen et al., 2016). These long generation times yielded N_e estimates 7.5× smaller than if a 20 years generation time was used. It is important to note that long-term N_e estimates are largely only applicable for comparative, rather than conservation purposes. Nevertheless, these scalar problems will remain a challenge, even with genomic advances, until firm generation times for Greenland sharks are determined.

Estimates of mutation rates in elasmobranchs are considered to be among the slowest in the animal kingdom (Martin et al., 1992). To date, mutation rates for *Somniosus spp.* Are unknown. Consequently, much of the dating for speciation times are hypothetical, however, the accumulation of genome-wide variation among multiple

Greenland shark individuals holds promise for estimating *Somniosus*-specific mutation rates. Obtaining approximate timing of speciation events, population expansions and reductions, and other genus-specific events using genetic methods will continue to be problematic until accurate mutation rates can be estimated.

Advances in population genomics, including complete mitogenomes, nuclear genomes, and genotype-by-sequencing approaches, appear promising for detecting population structure and evolutionary relationships for the Greenland shark and Somniosids in general. The most desirable nuclear molecular markers are those that permit detection and spatial delineation of populations (Ahonen et al., 2009). Such resolution is critical for determining evolutionarily significant units (ESUs; **Table 2.2**) or management units for conservation and management planning (Moritz, 1994). Genomic and genetic resources, such as numerous single nucleotide polymorphism (SNP) loci and highly polymorphic nuclear microsatellites, may provide the tools for determining the number of extant populations and the extent of connectivity among them (Milano et al., 2014). Novel sampling methodologies, such as the collection of external parasites to obtain host mitochondrial DNA sequences (Meekan et al., 2017), have proven effective for obtaining genetic samples for such analyses. These invertebrate DNA (iDNA) sequences have helped resolve the genetic structure and connectivity of global whale shark populations (*Rhincodon typus*; Meekan et al., 2017) and could be similarly applied using copepods sampled from parasitized Greenland sharks. While the spatial scale of elasmobranch populations varies widely from species to species, the geographical range of Greenland shark populations is likely far-reaching. The coupling of population genomic structure for *S. microcephalus* in the Atlantic and beyond, with movement data for analyzed individuals, will yield the most accurate distribution data for this species.

Despite growing conservation concerns for many shark species, the assignment of conservation status and the effective management of at-risk populations is commonly hindered by a lack of knowledge of stock structure and estimates of absolute population size. Detailed examination of the genomic structure of Greenland shark populations (using non-lethal biopsies or iDNA; Meekan et al., 2017) might allow researchers to define genetically distinct stocks, thereby supporting the delineation of appropriate management boundaries and multinational agreements. Furthermore, the examination of genetic relatedness among conspecifics is becoming an increasingly popular tool to estimate total population abundance (**Table 2.1**). For example, a recent study used genetic analyses to identify half-sibling pairs (HSPs) and unrelated pairs (UPs) to estimate abundance and survival rates of adult white sharks in Eastern Australia and New Zealand (*Carcharodon carcharias*). These data were further supplemented by acoustic tag data to estimate juvenile survival rates. Ultimately this method provided direct estimates of total abundance across both spatial and temporal life-history gradients (Hillary et al., 2018) and could similarly be used to assess Greenland shark populations.

2.5 Movement Ecology

Data on Greenland shark movements have been primarily recorded using a variety of telemetry technologies. Early work involved active short-term acoustic tracking of sharks under ice (Skomal and Benz, 2004; **Figure 2.3F**) and in estuarine waters (Stokesbury et al., 2005; Gallant et al., 2016). These tracks recorded vertical movements and light-based depth preferences, indicating that the Greenland shark is not strictly a demersal species. More recently, acoustic tracking in the St. Lawrence Estuary revealed that vertical movements into shallow and warmer water coincided with the pre-dawn high tide (Gallant et al., 2016). Archived depth records from pop-off archival satellite tags have also captured Greenland sharks swimming in the water column in deep-water offshore regions of the Arctic and North Atlantic (Campana et al., 2015a). These records demonstrate a preference among Greenland sharks for greater depths at lower latitudes (mean time-weighted depth over 6 h was 367 ± 4 m for Arctic sharks, compared to 949 ± 10 m for N. Atlantic sharks) and revealed long-distance horizontal movements, including one shark that traveled 1015 km over 125 days (Campana et al., 2015a).

Past studies using biotelemetry to record Greenland shark movements have largely relied on two methods, mobile acoustic tracking (Figure 3F) and archival satellite telemetry (**Figures 2.3C, D**); two approaches that require researchers to sacrifice either monitoring duration or data resolution. For example, active acoustic tracking can provide fine-scale horizontal movement data, but over limited timespans (hours or days; Skomal and Benz, 2004; Stokesbury et al., 2005; Gallant et al., 2016). In contrast, satellite tags can remain on animals for periods of up to several months (Stokesbury et al., 2005; Campana et al., 2015a), but produce only straight-line trajectories of tagged animals (via extrapolation between the location of animal capture and the ARGOS location transmitted by satellite tags following their pre-programmed release). Knowledge of the locations and timing of movement pathways, aggregation sites, and areas of ecological importance for Greenland sharks (*e.g.,* feeding grounds, and nurseries) therefore remains limited. Understanding the biological significance of movement behaviors is consequently difficult to assess and will require further study using available technologies and experimental design innovations.

The application of extensive passive acoustic telemetry infrastructure (fixed receivers that detect tagged individuals within their detection range; Heupel et al., 2005; Hussey et al., 2015b) and long lifespan transmitters (~10 years; **Figure 2.3E**) provides one solution to examine the long-term movements of Greenland sharks over a range of spatial scales. By combining multi-year records of animal detections with environmental data (ice cover, temperature, salinity, and dissolved oxygen), it will be possible to determine the spatiotemporal scales of predictable horizontal movements. Specifically, these data will delineate migration routes and activity hotspots as well as the environmental factors driving observed behaviors. The continued growth of a large-scale network telemetry approach in the Arctic (Hussey et al., 2015b) will promote collaborative data storage and handling and will rapidly increase data collection. For example, a telemetry network established in Baffin Bay was designed by the Ocean Tracking Network (OTN) in collaboration with the Canadian fishing industry and the Department of Fisheries and Oceans Canada (DFO) and is maintained by the joint efforts of all three groups (Cooke et al., 2011).

Innovative experimental designs, including the novel application or combination of existing telemetry technologies, can also allow researchers to overcome some of the limitations of tag design. For example, the attachment of multiple timed-release mark-report satellite tags (mrPATs, Wildlife Computers; **Figure 2.3C**) to individual sharks, has allowed the detection of a potential migration pathway and revealed synchronicity in Greenland shark movements (Hussey et al., 2018). The intermediate location estimates provided by this approach (typically not captured by satellite tag studies on non-surfacing animals) increased the resolution of recorded movement trajectories and provided data which are key for identifying suitable locations for the deployment of future acoustic telemetry infrastructure (Hussey et al., 2018). Furthermore, by combining a variety of telemetry technologies on individuals (*e.g.*, satellite tags, acoustic transmitters and receivers, and accelerometers; **Figures 2.3A, B**), researchers can compare movement behaviors at different data resolutions and timescales, informing habitat use, environmental conditions, and intra- or interspecies interactions, while maximizing the data collected for each tagged individual (Holland et al., 2009; Meyer et al., 2010; Hussey et al., 2018).

Despite rapid advances in telemetry technology and applications, capturing the ranges and movements of extremely long-lived species will require continued improvements in equipment design to increase tag longevity and the maximum depth ratings of telemetry equipment. Technological developments such as piezoelectric energy harvesting, which powers battery-free acoustic tags using the flexing motions of swimming fish (Li et al., 2016), will alleviate the limitations imposed by tag battery life. Additionally, mobile monitoring using animal-borne transceivers or autonomous vehicles (gliders; Lennox et al., 2017) will increase the coverage of telemetry studies and maximize potential data retrieval. Acoustic transceivers (VEMCO Mobile Transceiver; VMT) are transforming animals into mobile receivers capable of detecting other tagged individuals (Lidgard et al., 2012; Baker et al., 2014; **Figure 2.3B**) and have, thus far, been used to detect conspecific interactions in remote habitats (Holland et al., 2009) and seasonal patterns in group dynamics (fission–fusion behavior; Haulsee et al., 2016).

However, these methods currently require the animal to be recaptured to recover the tag and associated data. The development of Bluetooth technology linking VMTs and pop-off archival satellite tags (following the approach of Lidgard et al., 2014) will allow the remote transfer of animal detection data from VMTs to ARGOS satellites, eliminating the need for tag retrieval. This will thereby reveal interactions between Greenland sharks and other tagged animals, providing insight into their feeding and predatory behaviors (see section “Behavior”). Further advancement of archival satellite tags, including the recording of high-quality oceanographic data and faster data transmission to ARGOS satellites (increasing the volume of data transmitted and received), will also improve our understanding of environmental factors influencing the spatial habitat use of Greenland sharks.

Understanding the seasonal horizontal movements and spatial habitat use of Greenland sharks is critical for marine spatial planning (*e.g.*, ATLAS case study for Davis Strait, Eastern Arctic). Large-scale movements recorded by acoustic and/or satellite telemetry (tied with genomic data to identify population units, see section “Population Genetics and Genomics”) will help to refine our understanding of broad-scale Greenland shark distributions, allowing for the establishment of bilateral or multilateral agreements between nations or via Regional Management Organizations (RFMOs, see section “Management”) to manage at the population level (**Table 2.1**). At a finer scale, telemetry approaches will allow high-use or hotspot areas to be identified, and predictable movement patterns to be defined. These data, along with the distributions of potential threats (such as fisheries activity), can be integrated into predator-prey models (McClellan et al., 2009) which will indicate the spatial and temporal extent of regions that should be avoided or where fishing should be time-restricted during periods of increased Greenland shark presence. If necessary, this information would allow the implementation of precautionary measures such as Dynamic Area Management (DAM; NOAA, 2002) to reduce the likelihood of excessive bycatch (**Table 2.1**). Developing an understanding of the environmental drivers affecting Greenland shark movements will also improve our ability to predict how these patterns will be modified under various climate change scenarios, further directing the implementation of precautionary measures. Systematic conservation planning using spatial prioritization software tools, such as Marxan (Ball et al., 2009), will provide an approach to integrate these data to produce direct management advice (Metcalfe et al., 2015; **Table 2.1**).

2.6 Behaviour

To date, direct observations of Greenland shark behavior are extremely limited. Our understanding of their foraging mechanisms and predatory capabilities are largely based on combined evidence from movement records (see section “Movement Ecology”) and dietary analyses (see section “Diet and Trophic Ecology”). A single study on the three-dimensional movements of Greenland sharks recorded by high-resolution data loggers reported the slowest observed mean swim speed (0.34 ms^{-1}) and tailbeat frequency (0.15 Hz) relative to size for any fish species, leading researchers to question how they might catch much faster-moving prey (Watanabe et al., 2012). While scavenging behavior has been well documented (*e.g.,* inertial suction feeding from a demersal pot, Grant et al., 2018; photo evidence of Greenland sharks feeding on carrion at the surface, MacNeil et al., 2012; see section “Diet and Trophic Ecology”), direct observations of active predation have yet to be recorded. Despite this fact, several lines of evidence, including freshly ingested seal remains in Greenland shark stomachs and bite marks observed on live seals and overwintering beluga whales (*Delphinapterus leucas*), suggest that active predation on fastmoving prey like marine mammals does occur (Fisk et al., 2002; Leclerc et al., 2012; MacNeil et al., 2012; Nielsen et al., 2014). Members of the Inuit community of Pangnirtung (Nunavut, Canada) have also documented Greenland sharks scavenging seals and beluga from nets and have reported their belief in the shark's ability to capture and consume newborn seal pups (based on whole specimens found in shark stomachs) and to attack adult seals visiting breathing holes in the ice (from observations of bite wounds; Idrobo and Berkes, 2012). Given their observed slow swimming speed, it is hypothesized that sharks may adopt a stealth approach to target seals when they rest underwater or at the surface (Skomal and Benz, 2004; Watanabe et al., 2012).

With the vision of Greenland sharks in the Arctic considered to be impaired by copepod parasites (*Ommatokoita elongata*; Berland, 1961; Borucinska et al., 1998; Skomal and Benz, 2004; **Figure 2.4B**) and their slow swim speeds (Watanabe et al., 2012), the mechanism of active predation remains unknown. Consequently, the primary role of this species as a predator or scavenger of marine mammals has not been established (Bigelow and Schroeder, 1948; Ridoux et al., 1998; Lucas and McAlpine, 2002; Horning and Mellish, 2014), despite the importance of this information to our understanding of their true ecological role.

Another key question concerns the feeding frequency of Greenland sharks, particularly in relation to their metabolic rate and energy budgets. Given their large body mass, ectothermic physiology, and cold-water habitat, these sharks are likely to have extremely low mass-specific metabolic rates as a result of slow growth, long life spans (Nielsen et al., 2016), and slow swimming speeds (Watanabe et al., 2012). Seals provide a highly energy-rich food due to their large body size and high fat content (Stirling and McEwan, 1975; Addison and Stobo, 1993; Lucas and Natanson, 2010). It is possible, therefore, that Greenland sharks could survive for several months without feeding following the consumption of such energy-dense prey. The consumption rate of teleost prey (*e.g.,* Atlantic cod, *Gadus morhua*, or Greenland halibut; Nielsen et al., 2014) by Greenland sharks may also be much lower than that of other large sharks (time scale of days rather than hours).

The frequent vertical movements exhibited by Greenland sharks raise additional questions over the physiological and metabolic costs of inhabiting and transitioning between shallow and deep-water environments and the factors influencing such movements. Deep-sea sharks rely on a high liver mass to provide energy storage for ovary production during maturation, however, at shallow depths, this large proportion of fatty tissue (relative to body mass) results in positive buoyancy, potentially leading to a higher energetic requirement during descent (Nakamura et al., 2015). Further insight into the energetic costs of these movements may help to resolve questions regarding the frequency of feeding and quantity of prey intake required to maintain them.

To address questions surrounding feeding mechanisms and frequency, direct observation of interactions and hunting behavior using animal-borne video cameras (*e.g.,* Shark Tag camera; Kukulya et al., 2015) or other technologies (*e.g.,* active sonar) are needed. In recent years, telemetry advances have increasingly allowed indirect observations of animals in remote environments (Hussey et al., 2015b). For instance, active predation of pinnipeds by Pacific sleeper sharks was inferred from post-mortem temperature records collected by dual life history tags (LHX tags) implanted in Stellar sea lions (Horning and Mellish, 2014). Camera-bearing AUVs, such as Remote Environmental Monitoring UnitS (REMUS), have provided unique observations of the feeding behavior of white sharks *in situ* (Skomal et al., 2015) and could be easily adapted to monitor Greenland sharks. Several other technologies could provide indirect methods of recording Greenland shark interactions with conspecifics and potential prey. For example, through the deployment of hydrophones that record ambient noise on sharks (D-tag or Acousonde; Oleson et al., 2010), it may be possible to assess shark proximity to vocalizing marine mammals (sperm whale, *Physeter macrocephalus*, narwhal, *Monodon monoceros*, and ringed seal, *Pusa hispida*). In addition, recoverable VMT packages or satellite-linked units deployed on Greenland sharks (see section "Movement Ecology") could provide data on co-occurrence and the potential rate of interactions among tagged sharks, and between sharks and potential prey species equipped with acoustic tags (*e.g.*, Greenland halibut, Arctic skate, *Amblyraja hyperborea*, and narwhal; Broell et al. personal communication).

The combined use of accelerometers and animal-borne cameras on individual sharks provides one possible approach to examine the cost of vertical movement and determine the feeding frequency of Greenland sharks. For example, following the use of this technology on two deep-water species (bluntnose sixgill shark, *Hexanchus griseus*, and prickly shark, *Echinorhinus cookei*), researchers suggested that the positive buoyancy exhibited by sharks in shallow water may facilitate upward migrations or hunting near the surface, but may also lead to variable costs related to the habitat depth occupied. While this approach can help to infer the energetic costs associated with vertical movement (including potential foraging behaviors), to fully understand the energetic requirements of this species it will also be necessary to record fine-scale foraging behavior (actual feeding events) for sufficient periods of time (days to weeks). For example, acceleration-triggered video cameras allowed the identification of the individual feeding attempts of deep-diving elephant seals (Naito et al., 2017), providing a promising approach to capture low-frequency events given technological constraints (*e.g.,* logging duration of video tags and attachment of large tag packages for long durations). Modified pop-up archival tags that are placed in the stomach of the animal (through ingestion with bait) and record stomach pH (Papastamatiou et al., 2007) or bulk electrical impedance and stomach temperature (Meyer and Holland, 2012) also provide unique methods to address this question.

Direct observations of feeding behavior on free ranging prey and interactions with various forms of fishing gear will provide further insight into the development of deterrents, gear adaptations, and bait restrictions to reduce Greenland shark bycatch. Importantly, fine-scale movement data recorded by accelerometers attached to fishing gear or deployed on animals can also be used to assess behavioral responses to fisheries capture (Gallagher et al., 2016; Bouyoucos et al., 2017) and can provide evidence of post-release recovery and survival following capture and release (Brownscombe et al., 2013; **Table 2.1**). This method (using time-series vertical dive data recorded by animal-borne accelerometers) is currently being used to determine survival rates and the time required for Greenland sharks to return to normal behaviors following release from capture by bottom longlines (Watanabe et al., personal communication).

2.7 Physiological adaptations

Due to the Greenland shark's large size and remote habitat, which have precluded sophisticated *in vivo* experimentation and captive studies, many studies are conducted under field conditions that favor experiments on isolated tissues rather than whole animals. As a result, the basic physiology of the Greenland shark remains largely a mystery (MacNeil et al., 2012; Herbert et al., 2017).

While the cardiovascular system underlies every facet of an animal's life, relatively few studies have examined this in the Greenland shark. A recent study on the whole blood of Greenland sharks noted that their blood properties (high oxygen affinity and low Bohr effect) were typical of sluggish elasmobranchs (Herbert et al., 2017). However, using isolated hemoglobins, the blood was found to have a relatively low affinity and consist of three hemoglobin isoforms with no functional differences (Russo et al., 2017). This analysis suggested that cellular changes in allosteric effectors may be important for controlling the O_2 transport properties of the blood. Additionally, in an investigation of the stress response of Greenland sharks caught on bottom longlines, capture-induced changes in blood glucose and lactate values were found to be variable and were weakly related to capture depth (lactate) and body length (glucose; Barkley et al., 2017).

Characteristics of the Greenland shark's heart and blood vessels are also beginning to emerge. Greenland sharks were found to have a low intrinsic heart rate paired with a high ventricular volume (measured *ex vivo*; Shiels et al., 2018) (**Figure 2.4C**). Histological analysis of heart samples showed significant fibrosis that increased with age; a preliminary analysis revealed no evidence of atherosclerosis. Efforts to quantify details of heart performance using isolated cardiac heart strips (Larsen et al., 2017) have proved to be largely unsuccessful as the tissue does not remain viable for long periods. In heart strips that appeared to be contracting normally, a single contraction/relaxation cycle (*i.e.*, a twitch) required 3–5 s to complete at 5°C, suggesting that maximal heart rate ranges from 12 to 20 beats/min (in agreement with Shiels et al., 2018). While blood pressure in Greenland sharks has never been directly measured, it has been estimated by analyzing the relative amounts of elastin and collagen in the wall of the ventral aorta and measuring its compliance characteristics over a range of pressures (Shadwick et al., 2018). These data suggest that the Greenland shark's average blood pressure is approximately 2.3–2.8 kPa, much lower than other slow swimming sharks, such as the epaulet shark, *Hemiscyllium ocellatum* (3.9 kPa), or catshark, *Scyliorhinus canicula* (5.3 kPa), where it has been directly measured (Taylor et al., 1977; Speers-Roesch et al., 2012).

Further physiological studies have largely focused on systems which are likely to play an important role in foraging behaviors. Olfactory cues are typically important for locating prey, especially where visual cues are limited. An anatomical study of the olfactory rosette in the Greenland shark indicated that while the arrangement of the olfactory lamellae and epithelium are similar to those found in benthic\slow swimming animals, the relatively large olfactory epithelium surface area is more reflective of a bentho-pelagic animal (Ferrando et al., 2016).

Preliminary biochemical assays and work loops (force *vs.* length curves used to determine the mechanical work of muscle fibers) indicate that both red and white skeletal muscle fibers have very low metabolic capacities and contraction (twitch) rates (Bernal personal communication). This suggests that they are unable to sustain high levels of either anaerobic or aerobic muscle contraction for extended periods. These data consequently raise questions over how Greenland sharks actively forage in the water column for teleosts and marine mammals (Fisk et al., 2012; MacNeil et al., 2012; Nielsen et al., 2014, see section "Behavior").

While sharks, in general, have good vision, little is known about sharks' visual adaptations to their environment and how this is impacted by their ecology and habitat (McComb et al., 2010). Greenland sharks are thought to have poor vision, potentially as a result of corneal damage produced by the attachment of the parasitic copepod, *O. elongate* (Berland, 1961; Borucinska et al., 1998; **Figure 2.4B**) as well as the dark environment they inhabit (300–500 m; Nielsen et al., 2014). In the absence of active parasitism, sharks may still possess scar tissue on the cornea from previous infections, however, no evidence of a correlation between shark size/age and degree of corneal damage has yet been recorded (Nielsen personal communication). Additionally, while a high incidence of copepod parasitism has been reported at high latitudes in the Eastern Canadian Arctic and off eastern and western Greenland (~90% of sharks showing parasitism, Steffensen personal communication), a much lower incidence of active parasitism has been recorded in the St. Lawrence Estuary and in waters off southern Atlantic Canada (<10% of observed sharks, Gallant personal communication, and no parasitized sharks observed, Campana personal communication, respectively). Despite this observed spatial disparity in copepod presence/absence, the degree of corneal damage present in sharks from these discrete locations has yet to be examined thoroughly. Systematic investigations of this disparity, and of the cumulative effects of multiple parasitic infections on corneal structure and vision are thereby required. Furthermore, novel records of vision-associated behaviors (defensive posturing) performed by non-parasitized sharks in shallow waters (St. Lawrence Estuary; Harvey-Clark et al., 2005), and evidence to suggest that Greenland sharks are potential active predators (Watanabe et al., 2012; Nielsen et al., 2014), further warrant a thorough understanding of their visual system.

Despite the limitations precluding *in vivo* experimentation, future anatomical studies and *in vitro* experiments will lead to important insights with regards to whole animal function. For example, studies directed at defining skeletal muscle characteristics (fiber type, distribution, contraction rates and pH buffering properties; Figure 4D), and cardiorespiratory characteristics (*e.g.*, heart rate, stroke volume, blood pressure, ventilation rate, ventilation volume, extraction efficiency, and blood buffering capacity; **Figure 2.4C**) will be important in building a complete picture of the Greenland shark as a top predator in the Arctic ecosystem. Understanding these physiological attributes is also key for improving knowledge of the mechanisms driving longevity.

Established in vitro techniques will also facilitate future examination of the visual system in Greenland sharks (**Figure 2.4A**). Approaches such as electroretinography could be used to determine spectral/luminous sensitivities and temporal resolution (Kalinoski et al., 2014), while microspectrophotometry can elucidate the type and distribution of visual pigments (Hart et al., 2005). Of particular interest, given the long-lived nature of this species, is the study of ontogenetic changes in brain organization that might occur over 200 years, potentially altering sensory acuity and therefore the relative importance of senses such as vision and olfaction over individual lifespans (Lisney et al., 2017).

Further study of the importance of olfaction and electroreception for prey location will provide insight into the foraging behavior of Greenland sharks, including factors affecting incidental capture by fishing gear. Specifically, age-related changes in the olfactory epithelium could be examined given documented changes in other species (Ferrando et al., 2016). Greenland sharks also appear to have a well-developed network of electroreceptors (Ampullae of Lorenzini) that allow them to detect the bio-electrical activity of animals at close range (Kalmijn, 1971), but their arrangement has yet to be described. Given the lack of response exhibited by Greenland sharks presented with electropositive metals (Grant et al., 2018), further study of the sensitivity of their electroreceptors may be beneficial for the development of effective hook deterrents to mitigate bycatch.

Understanding the role of the Greenland shark as a potential apex predator also requires accurate measurement of its metabolic rate and scope (aerobic and anaerobic) during resting, swimming, and digestion cycles (**Figures 2.4E, F**). In addition to establishing rates of energy expenditure for these activities, metabolic rate has also been shown as a determinant of life span based on temperature and body size (Gillooly et al., 2001). Preliminary studies on ~250 kg Greenland sharks found that they did not have an unusual metabolic rate (Steffensen et al., personal communication; **Figure 2.4E**) compared to what could be expected given its large size and body temperature. More metabolic studies are warranted, particularly comparing the resting metabolic rate of starved *vs.* fed sharks to evaluate the time course and energy expenditure associated with digestion (Specific Dynamic Action, SDA; Sims and Davies, 1994; Ferry-Graham and Gibb, 2001).

A greater understanding of these physiological traits and energetic requirements will ultimately lead to improved species management for both Greenland sharks, and their commercially targeted prey species. Specifically, there is a fundamental need for baseline (unstressed) values for virtually all blood parameters from Greenland sharks and for the accurate quantification of capture stress. Furthermore, understanding the bioenergetic requirements of individual Greenland sharks (via field measurements of metabolic rate and direct observations of consumption rate, see section “Behavior”) will help to estimate the energetic needs of sharks at the population level. This could be crucial for informing harvest levels (*e.g.,* Total Allowable Catches, TAC) of targeted Greenland shark prey species to ensure that the remaining biomass is resilient to sustained fishing effort (**Table 2.1**).

2.8 Diet and Trophic Ecology

The diet of Greenland sharks includes an impressive diversity of prey (Yano et al., 2007; McMeans et al., 2010; Leclerc et al., 2012; Nielsen et al., 2014; Nielsen, 2017). For example, stomachs of 39 Greenland sharks from western Greenland waters contained 25 different fish species, at least 3 pinniped species, and several groups of invertebrates (molluscs, echinoderms, decapods; Yano et al., 2007). Live prey capture is possible (see section “Behavior”), however, scavenging of marine mammal carrion (Williamson, 1963; Beck and Mansfield, 1969; Leclerc et al., 2011) and cannibalism of conspecifics captured in fishing gear (Jensen, 1948; Nielsen et al., 2014) are known to occur. Several reports indicate that Greenland sharks consume both benthic and pelagic prey (MacNeil et al., 2012), and the simultaneous occurrence of both prey types in the diet of Greenland sharks is consistent with diurnal behavior observed using biotelemetry (Campana et al., 2015a).

Spatial variations in the relative importance of pelagic prey (*i.e.*, a higher proportion of pelagic fishes in shark stomachs from Iceland *vs*. Canadian Arctic) have also been reported, however, this may reflect differences in sampling method (gillnet and trawl *vs.* bottom longline) or L_T (mean ± S.E. 416 ± 25; 284 ± 44 cm, respectively; Fisk et al., 2002), rather than true dietary variations (MacNeil et al., 2012). Stable isotopes, fatty acids, and biomagnifying contaminants confirm a high trophic position and consumption of diverse prey types (Fisk et al., 2002; McMeans et al., 2010, 2015; Hussey et al., 2014). Geographical variation in diet further suggests that Greenland sharks exhibit a flexible response to variation in prey availability (McMeans et al., 2013a; Nielsen et al., 2014). However, some prey selectivity may occur because some abundant fish species (*e.g.*, redfish; *Sebastes spp.*) are rarely present in shark stomachs from Greenland waters (Nielsen et al., personal communication). Stomach contents and biochemical markers also provide evidence that larger sharks consume more teleost and marine mammal prey compared to smaller sharks (less than 200 cm L_T; Yano et al., 2007; McMeans et al., 2013a; Nielsen, 2017), which have been found to feed predominantly on lower trophic level prey such as squid (Nielsen, 2017).

Greenland sharks are mobile, opportunistic top predators that obtain and couple energy from multiple habitats within an ecosystem (McMeans et al., 2013b) and across geographically distant ecosystems (see section "Movement Ecology"). Although their effect on food web dynamics has yet to be quantified, existing food web theory suggests that mobile, opportunistic top predators are important for food web stability (McCann et al., 2005; Rooney et al., 2006). Empirical examples for this theory include Atlantic cod (*G. morhua*), which are thought to stabilize the ecosystem by preventing oscillatory, overshoot dynamics in their prey (Frank et al., 2011). Given their broad distribution and potential capacity for active predation (see section "Behavior"), Greenland shark populations could play a similar role in marine food webs, despite expected slow metabolism and low consumption rates (see section "Behavior"). While it has been suggested that Greenland sharks may be a significant source of mortality for some seal populations (Leclerc et al., 2012), the effects of consumption by Greenland sharks on prey populations must be examined further. This is of particular importance, as facultative scavenging may amplify the top-down trophic effects exerted by Greenland sharks on their food web because high-quality carrion can inflate predator biomass and increase a predator's capacity for prey control (*e.g.,* in wolves; Wilson and Wolkovich, 2011). As both potential predators and scavengers of many prey taxa, Greenland sharks could therefore have widespread effects on food webs throughout the Arctic and North Atlantic. A lack of evidence to define potential subpopulation dietary specialization, as well as further uncertainty surrounding the role of extreme longevity in nutrient and energy transfer in marine food webs also indicate the potential value of more detailed study of the trophic role of Greenland sharks in Arctic marine environments.

Future work will need to quantify the type (active predation *vs.* scavenging) and frequency of trophic interactions between Greenland sharks and their prey (**Table 2.1**). Video observations and tracking technology (see section "Behavior"), combined with non-lethal sampling of tissues (blood and muscle) for dietary analysis (stable isotopes, amino acid compound specific isotope analysis, and fatty acids) will allow a more comprehensive understanding of Greenland shark diet and their functional role within food webs without the need to sacrifice individuals. Through a combination of accurate estimates of diet, field measurements of consumption and metabolic rates (see sections “Behavior” and “Physiological Adaptations,” respectively), detailed movement behaviors (see sections “Movement Ecology” and “Behavior”) and abundance estimates (see section “Demographics and Life History”), it will be possible to quantify energy flow and trophic transfer efficiencies, shedding light on Arctic food web dynamics (*e.g.,* biomass structure – pyramid/inverted pyramid and interaction strengths) that may prove important for understanding past and future food web stability (McCann et al., 2005). Geographical comparisons of biomass structure (the distribution of biomass across trophic levels) could be undertaken to study how variation in Greenland shark abundance regulates these food webs. A particularly exciting possibility is to synthesize food web data (*i.e.,* predator prey relationships and abundance data through time), which can then be used to estimate indices of stability (*e.g.*, the coefficient of variation of prey population dynamics; Korpimäki, 1984). Such an effort would provide quantitative data on how Greenland shark density and foraging behavior (*e.g.,* the extent of cross habitat foraging) influences food web dynamics.

Ecosystem models (EcoPath and EcoSim) can help predict the effects of various fisheries management decisions (and associated changes in fishing pressure) on marine food webs (Travers et al., 2010). Through these models, diet and abundance metrics can be used to predict the potential effects of changes in Greenland shark abundance on prey species (including those affected by commercially harvest, *e.g.,* Greenland halibut). Bycatch limits for Greenland sharks could then be set at levels to ensure that the remaining shark biomass is sufficient to maintain ecosystem function while also maintaining adequate prey biomass (Table 1).

2.9 Threats to Greenland Shark Populations

Despite occupying great depths and remote, polar regions, Greenland sharks experience many of the same anthropogenic and climatic stressors as other long-lived marine species (*e.g.*, fisheries, vessel traffic, seismic surveys, pollution, and climate change; Clarke and Harris, 2003; Halpern et al., 2008; Davis et al., 2013). This may be particularly true for sharks inhabiting coastal regions of the North and Norwegian seas and the North American eastern seaboard; areas that are predicted to be cumulatively impacted by numerous anthropogenic drivers of ecological change (Halpern et al., 2008). Importantly, given their *K*-selected nature, impacted Greenland shark populations will likely be slow to recover.

Of these threats, fisheries have the greatest impact on Greenland shark populations. Directed fisheries for Greenland sharks existed in Norway, Iceland and Greenland from the 1600s to the mid-1990s (Davis et al., 2013). Catch rates grew to 15,000 Greenland sharks per year by the end of the 18th century with a peak catch of 32,000 individuals in Greenland in 1910 (Davis et al., 2013). Greenland shark catches continue at much lower levels today (see section "Demographics and Life History"). This includes Greenland shark bycatch in fisheries targeting other species, particularly Greenland halibut or shrimp, which occurred during the period of directed fishing and have continued since (Davis et al., 2013). Bycatch is typically returned to the ocean, but the proportion of animals that survive varies with fishing gear type, fishing duration, and handling method. A recent examination of Greenland shark bycatch in Canada found that 36% of sharks caught in bottom trawls (Greenland halibut and northern shrimp fisheries) and 16% of sharks caught on benthic longlines (Greenland halibut fisheries) were already dead when released (North Atlantic Fisheries Organization [NAFO], 2018b,c) and the percentage of dead sharks increased with trawl duration (North Atlantic Fisheries Organization [NAFO], 2018c).

The threats posed by incidental capture are not limited to post-release mortality. Like many elasmobranchs, Greenland sharks are often viewed as competitors for commercially valuable species by harvesters. For example, Greenland sharks that feed from and are incidentally captured by bottom longlines can become entangled in the fishing gear and rolling behavior can result in the mainline becoming tightly wrapped around the caudal peduncle, complicating release efforts (Edwards personal observation; **Figures 2.5A, B**). For this reason, Greenland sharks are often considered a nuisance species in commercial fisheries and entangled individuals may be removed by severing the caudal fin (Davis et al., 2013). Historically, Greenland sharks in the Saguenay Fjord were hauled out as trophies, but now they must be released while still in the water. This law has been strictly enforced by the Department of Fisheries and Oceans Canada since 2006 (Gallant personal communication).

Even in the absence of directed fisheries, the rate of interactions among Greenland sharks and commercial fishing gear can be expected to increase in coming years. Ongoing reductions in sea ice extent and duration in the Arctic and changes in the composition and productivity of Arctic marine communities (Clarke and Harris, 2003) are allowing existing fisheries (bottom longline, trawl, and gillnet) to expand northward into previously unfinished habitats and extend their fishing season, while also creating the potential for new fisheries to develop (Christiansen et al., 2014).

In addition to fisheries pressures, Greenland sharks can also be affected by chronic and acute changes in their environment from pollution, increased noise, and climate change; factors which are likely to affect most fish and marine mammals in the Arctic (Clarke and Harris, 2003; Huntington, 2009). Pollution from global atmospheric deposition, coastal communities, and vessels can affect Greenland sharks directly by impacting their physiological balances (*e.g.,* heavy metals, hormones, toxins; Strid et al., 2007, 2010; Corsolini et al., 2014) or indirectly by altering ecosystem productivity which can lead to eutrophication and reduced oxygen availability (*e.g.,* St. Lawrence hypoxic dead zone; Belley et al., 2010; Howarth et al., 2011). Alongside natural sounds from animals, tides and currents, anthropogenic noise from vessels and industrial development are increasing in the Arctic with unknown effects (Ivanova et al., 2018).

Mirroring this extensive list of potential threats to Greenland shark populations is a series of questions that must be addressed. In the absence of population size or demographic data, it is currently not possible to estimate the impacts of historical fisheries on Greenland shark populations (size, age, sex, or maturity trends), or to examine changes in population metrics (*e.g.,* recovery rate) following the cessation of directed fishing. In addition, when examining the available commercial bycatch data, it is important to consider potential inaccuracies. Large animals such as Greenland sharks are typically not weighed. Instead, bycatch records are generally limited to counts and may include supplementary data such as individual lengths, sex, and status (alive or dead). When weights are recorded, they are often a best guess based on the experience of the observer at estimating the weight of fish in a net.

There is also insufficient data to accurately estimate post-release mortality rates for bycaught Greenland sharks and to determine the effects of key factors such as gear type. While post-release mortality rates of up to 50% have been recorded in other sharks (as measured with PSATs; Campana et al., 2015b), this is known to vary widely across species. Additional data will therefore be required to accurately estimate the effects of incidental capture on Greenland shark populations and determine handling practices that will ensure optimum survival rates (see section “Behavior”).

While the precise impacts of indirect threats such as noise pollution and seismic surveys on Greenland shark behavior and physiology have not been quantified, sharks may need to adapt to changes in prey availability in areas where seismic surveys are conducted. Vessel noise can alter both short and long-term habitat use decisions by animals, affecting overall species distributions (Sarà et al., 2007; Slabbekoorn et al., 2010; McCarthy et al., 2011; Ivanova et al., 2018). For example, research in the Barents Sea has shown that seismic shooting can significantly affect fish distribution, local abundance, and catch rates (Engås et al., 1996). High intensity sounds from seismic surveys or pile driving could also have more direct impacts on individuals, causing sensory damage (and potentially death), leading to avoidance behaviors and changes in habitat use (Popper and Hastings, 2009).

Scientific efforts to increase our understanding of the many threats faced by Greenland shark populations and their surrounding ecosystems are underway. In an effort to improve the quality of data obtained from Greenland shark bycatch, DFO requested, on a trial basis, that at-sea observers use a statistical length-weight key to estimate

Greenland shark weight based on a measured length, along with criteria to assess condition.

Changes to fishing gear (Grant et al., 2018) and practices such as limiting set duration (Cosandey-Godin et al., 2014) have been examined as methods to reduce Greenland shark bycatch mortality. However, testing of additional bycatch mitigation strategies (*e.g.*, gear modifications such as modified mono-filament gangions) as well as the data required to monitor the status of Greenland shark populations (abundance and/or biomass indices, size and sex ratios; see section “Demographics and Life History”) will also be necessary for maintaining sustainable mortality levels. Bycatch records and video observations of Greenland sharks interacting with fishing gear (Grant et al., 2018) are invaluable for adapting gear to minimize the probability of shark capture or entanglement and to allow monitoring of the frequency of interactions. Similarly, data from telemetry and archival tags are revealing the horizontal and vertical movement patterns of Greenland sharks (see section “Movement Ecology”), which can be used to adapt fishing practices (*e.g.*, harvester avoidance of high use areas, DAM plans; NOAA, 2002).

Continuing to articulate the link between threats and Greenland shark population(s) status in the scientific literature is useful for fishery management and marine spatial planning. Furthermore, regular communication of Greenland shark research results to managers, stakeholders, listing organizations, and the general public is crucial for raising awareness of the role of Greenland sharks in Arctic ecosystems, and for drawing attention to the need for their effective management. This can be achieved through various forms of outreach, including publications/reports, presentations, media (social, radio, print, and television), community posters, student engagement, and music videos.

Fisheries managed by Arctic countries, NAFO, and ICES apply the precautionary approach to fishery management (Food and Agricultural Organization [FAO], 1996; North Atlantic Fisheries Organization [NAFO], 2004; Department of Fisheries, and Oceans [DFO], 2006, 2009; ICES, 2012). While full stock assessments are typically limited to species that are commercially harvested, a similar level of analysis and management for key bycatch species is being considered in some jurisdictions (Department of Fisheries, and Oceans [DFO], 2013) and should be considered for the Greenland shark. Ecosystem-based fishery management (EBFM) involves managing fisheries with consideration of supporting ecosystem components and impacts on marine habitats (*e.g.,* physical disruption and soundscape) and communities (*e.g.,* direct mortality, competition with predators), in addition to commercial harvests and stock status (Pikitch et al., 2004; Trochta et al., 2018). Incorporating Greenland sharks into EBFM frameworks would require an accurate understanding of the shark's role in the ecosystem and a model of community trophic linkages, data which are not currently available. EBFM also includes environmental drivers of ecosystem and animal productivity (*i.e.,* to rebuild and sustain populations, species, biological communities, and marine ecosystems at high levels of productivity and biological diversity while providing food, revenue, and recreation for humans; U.S. National Research Council, 1998). The full application of the EBFM approach to fisheries with Greenland shark bycatch will therefore require new information regarding the nature and magnitude of each driver's effects, both in isolation and in combination. Marine spatial planning that accounts for potential impacts on Greenland sharks will require the same data and analyses to be effective. In the meantime, multi-species stock assessment models provide one option to incorporate Greenland shark management actions into current directed fisheries management plans (Moffitt et al., 2016). Alternatively, trophic pyramid modeling provides a method in which catch limits are applied to trophic levels rather than individual species in an effort to reduce a fishery's impacts on overall community structure (Garcia et al., 2012, 2014; Froese et al., 2015; Burgess et al., 2016). Results from such modeling exercises can inform management decisions and be incorporated in fishery-level documents such as the Integrated Fishery Management Plans that are developed for Canadian fisheries (see section "Management"). Fishery-level documents can then be referenced by and linked to marine spatial planning initiatives at national and international levels to achieve integration among management sectors and activities.

2.10 Management

Laws and policies relevant to Greenland shark management occur

at global, regional and national levels.

2.10.1 Global

A fragmented array of global agreements and guidance documents have emerged to promote sustainable fisheries and marine biodiversity conservation in general (Russell and VanderZwaag, 2010; Techera and Klein, 2017), but shark-specific law and policy developments are limited to four main avenues (Davis et al., 2013). First, various shark species have been listed as endangered or threatened under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) with resultant international trade restrictions imposed through export and import permit requirements (Hutton and Dickson, 2000; CITES, n.d.). The Greenland shark has not been considered for CITES listing due to its conservation status, being categorized as near threatened under the IUCN Red List of Threatened Species (IUCN, 2017), and lack of trade concerns.

Second, under the Convention on the Conservation of Migratory Species of Wild Animals (CMS), a Memorandum of Understanding on the Conservation of Migratory Sharks (Sharks MOU) has been adopted that encourages signatories to apply precautionary and ecosystem approaches to shark conservation (CMS, 2016). A Conservation Plan, included in Annex 3 to the Sharks MOU, sets out numerous implementation actions that should be prioritized by signatory states including: improving migratory shark research and monitoring; strengthening controls over directed and non-directed shark fisheries; ensuring the protection of critical habitats and migratory corridors; and increasing public awareness of the threats to sharks (CMS, 2016). However, the MOU has limited application, and is only applicable to 29 listed shark and shark-related species, which does not include the Greenland shark (CMS, 2018a). Additionally, the MOU only has 48 signatories (CMS, 2018b), which do not include key Arctic states such as Canada, Iceland, Norway, and the Russian Federation (CMS, 2018b).

Third, the Food and Agriculture Organization (FAO) has adopted an International Plan of Action for the Conservation and Management of Sharks (Food and Agricultural Organization [FAO], 1999), which encourages states to adopt national plans of action for the conservation and management of sharks in directed or non-directed fisheries. Such plans often seek to minimize the unutilized incidental catch of sharks, contribute to the protection of biodiversity and ecosystem structure and function, and facilitate improved species-specific catch and landings data. States are further encouraged to assess implementation of national plans at least every 4 years and to consider, where appropriate, the development of sub-regional or regional shark plans.

A fourth global avenue of specific shark-related law and policy development is through the UN General Assembly and its adoption of annual resolutions on sustainable fisheries, which include paragraphs urging states and RFMOs (see section "Movement Ecology") to better protect sharks. For example, the sustainable fisheries resolution (Res. 72/72), adopted in December 2017, urges states to take multiple science-based measures to manage shark stocks including: setting limits on catch or fishing efforts, requiring the reporting of species-specific data on discards and landings, undertaking comprehensive stock assessments of sharks, and reducing shark bycatch and bycatch mortality. Regional Fisheries Management Organizations (RFMOs) with competence to regulate highly migratory species are urged to strengthen or establish precautionary, science-based, conservation and management measures for sharks.

2.10.2 Regional

A major regional development relevant to Greenland shark conservation was the conclusion in November 2017 of a draft Agreement to Prevent Unregulated High Seas Fisheries in the Central Arctic Ocean (U.S. Department of State, 2017). The Agreement, expected to be adopted by the five Arctic Ocean coastal states along with China, Iceland, Japan, South Korea, and the EU, aims to apply a precautionary approach to possible future commercial fisheries in the high seas of the central Arctic Ocean (CAO). The

Agreement pledges parties to not authorize their flagged vessels to conduct commercial fishing in the CAO until conservation and management measures for fish stocks are adopted by one or more regional or sub-regional fisheries management organizations. Within 2 years of entry into force, parties agree to establish a Joint Program of Scientific Research and Monitoring with the objectives of improving understandings of ecosystems in the CAO and of determining whether fish stocks might exist that could be harvested on a sustainable basis. Party meetings are to be held every 2 years to review implementation of the Agreement, to review all available scientific information and to consider whether to commence negotiations for one or more additional regional or sub-regional fisheries management organizations or arrangements. The Agreement holds promise to substantially expand knowledge of the CAO and adjacent ecosystems and to provide refuge for Greenland sharks from potential unregulated fishing in the high Arctic.

Three North Atlantic regional fisheries management organizations have also addressed shark conservation in limited ways (Davis et al., 2013). The Northwest Atlantic Fisheries Organization (NAFO) has adopted general shark conservation and enforcement measures (North Atlantic Fisheries Organization [NAFO], 2018a). Shark finning is prohibited by requiring shark fins to remain attached to carcasses, and for non-directed shark catches, parties are required to encourage the live release of sharks (especially juveniles) that are not intended for use as food or subsistence. Parties are urged to undertake research in relation to sharks including: ways to make fishing gear more selective, key biological and ecological parameters, life history, behavioral traits and migration patterns, and the identification of potential mating, pupping, and nursery grounds of key shark species. Since 2012, NAFO has required, to the extent possible, species-specific reporting of shark catches in the NAFO Regulatory Area with the amount of Greenland sharks caught in 2013 reported as 22.2 tons (North Atlantic Fisheries Organization [NAFO], 2014) and rising to 203.2 tons in 2016 (North Atlantic Fisheries Organization [NAFO], 2017). Not all shark catches have been reported to the species level and it is not known how many shark species were simply lumped into the category of dogfishes (North Atlantic Fisheries Organization [NAFO], 2017).

NAFO's Scientific Council, upon a request from the Commission, has been undertaking a review of the available information on the life history, population status, and current fishing mortality of Greenland sharks. Notably, at their most recent meeting held in June 2018, the Scientific Council (SC) made several suggestions, which included the prohibition of directed fishing and bycatch retention and the required release of live Greenland sharks captured within the NAFO Convention Area (North Atlantic Fisheries Organization [NAFO], 2018b). In addition, the SC recommended the promotion of safe handling practices by fishers, and that improvements be made to the reporting of all shark species by fisheries observers, including the collection of shark numbers, measurements (when feasible), and the recording of sex data and discard disposition (*i.e.,* dead or alive; North Atlantic Fisheries Organization [NAFO], 2018b). To reduce bycatch, the application of gear restrictions and modifications, and/or spatial and temporal closures (where appropriate) was also recommended (North Atlantic Fisheries Organization [NAFO], 2018b). Approval of these suggestions by the Commission is pending, and further discussion was scheduled to take place at the annual NAFO meeting in September 2018 (North Atlantic Fisheries Organization [NAFO], 2018b).

The North-East Atlantic Fisheries Commission (NEAFC) has adopted shark conservation measures similar to those of NAFO. NEAFC also prohibits shark finning, encourages the live release of sharks caught in non-directed fisheries, and requires annual reporting of shark catches (NEAFC, 2015). NEAFC continues to prohibit directed fishing for deep sea sharks, including the Greenland shark, in NEAFC's Regulatory Area and encourages parties to adopt prohibitions within national waters as well (NEAFC, 2017).

The International Commission for the Conservation of Atlantic Tunas (ICCAT) has adopted various recommendations relating to shark conservation over the years (Davis et al., 2013). Some of the most recent include recommendations on biological sampling for shark species where retention is prohibited (ICCAT, 2014) and on shortfin mako (*Isurus oxyrinchus*) porbeagle (*Lamna nasus*), and blue sharks (*Prionace glauca*) caught in association with ICCAT fisheries (ICCAT, 2013, 2015, 2016). No recommendations have been adopted specific to Greenland sharks, however, these are needed.

2.10.3 National

Besides a broad array of general legislative, regulatory, and policy provisions in support of sustainable fisheries and marine biodiversity protection (VanderZwaag et al., 2012; Sybersma, 2015), Canada adopted a National Plan of Action for the Conservation and Management of Sharks in 2007, which describes the Canadian legislative and regulatory framework for managing shark populations and fisheries, noting the importance of following precautionary and ecosystem approaches in future implementation (Fisheries, and Ocean Canada, 2007). Two limited references are made to the Greenland shark, noting the problem of Greenland shark bycatch and discards at sea in the Arctic region. The Plan commits Canada to move ahead with measures that increase knowledge about the life history and abundance of elasmobranchs in the Arctic, including the Greenland shark. Given the numerous knowledge gaps discussed in this paper, and the suspected implications of extreme longevity to limit the recovery of Greenland shark populations to disturbance, it is important that checks and balances are put in place to ensure that these research goals are met.

A Canadian progress report on implementation of the National Plan of Action for Sharks (NPOA-sharks), issued in 2012, provided little further information regarding Greenland shark conservation issues and efforts (Fisheries, and Oceans Canada, 2012). The progress report once again noted the bycatch and discarding reality in the Arctic and recognized the need for further research on the life history and abundance estimates. The report mentioned the completion of satellite tagging of Arctic shark species with results forthcoming. The report also noted that Canada was considering developing future projects to evaluate how changing Arctic conditions, such as climate change and increased shipping may affect shark species.

An integrated fisheries management plan (IFMP) for one of Canada’s main commercial fisheries in the Arctic has addressed Greenland shark bycatch in limited ways. The IFMP for Greenland halibut, effective in 2014, noted the ongoing problem of inaccurate bycatch reporting and the need to improve bycatch management (Fisheries, and Oceans Canada, 2014). The IFMP listed Greenland shark as a species of concern, noted that the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) had not yet assessed the conservation status of Greenland shark, and indicated the main bycatch management measure was to require release of incidental fish catches other than groundfish, and where alive, in a manner causing the least harm.

2.11 Conclusion

Organisms characterized by low productivity are particularly susceptible to overfishing and stock collapse and therefore are incapable of supporting more than nominal fishing mortality rates (Stevens et al., 2000). Despite historically high catch rates in some regions, Greenland sharks may be very sensitive to overfishing, even compared to other shark species. With recent evidence to support extreme longevity and conservative life history traits, coupled with their vulnerability to incidental capture by commercial fisheries, the sustainability of Greenland shark populations is of growing concern among fisheries management organizations. In spite of continued developments in the field of Greenland shark research, many questions still remain unanswered. To develop appropriate management actions aimed at preventing population declines, there is a current need to address these knowledge gaps through focused study and continued innovations in technology and experimental design. In this paper we identify key biological questions from several fields of Greenland shark research and, by drawing from recent tools and techniques from the broader literature, we propose a number of strategies which could be used to address these key questions. In particular, knowledge of the generation times, migration patterns, stock status, the locations of mating grounds and detailed information on reproduction of Greenland sharks will improve our ability to effectively manage this long-lived species. Importantly, vulnerability to population decline and the biological traits that influence it are common among long-lived species. Consequently, the critical parameters outlined in this paper and proposed methodologies to quantify them are likely applicable to most long-lived aquatic species. There is a need for researchers to use both traditional and creative approaches to engage stakeholders, build trust, and enhance collaboration, actions that will ultimately lead to improved management of this species, and long-lived species in general.

2.12 Author Contributions

JE was responsible for contacting and coordinating the collaborating authors, and wrote the Abstract, Introduction, Methods, and Movement Ecology section (with NH). The Demographics section was written by BD, JN, and SC. Population genetics and genomics was written by RW and KP. Behavior and interactions was written by YW, FB, and GS. JS, PB, and JC wrote the Physiological adaptations section. Diet and trophic ecology was written by BM, JN, JC, and JS. The Threats section was written by KH, the outline was created by EH, and comments were provided by EH, YW, and SC. The Laws and Policies section was written by DV. Table 1, which formed the basis for the structure of this paper was created by EH and NH and revised by JE. Final edits were completed by MM, JE, and NH. All authors contributed to the writing and editing of the final manuscript.

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TABLES/FIGURES

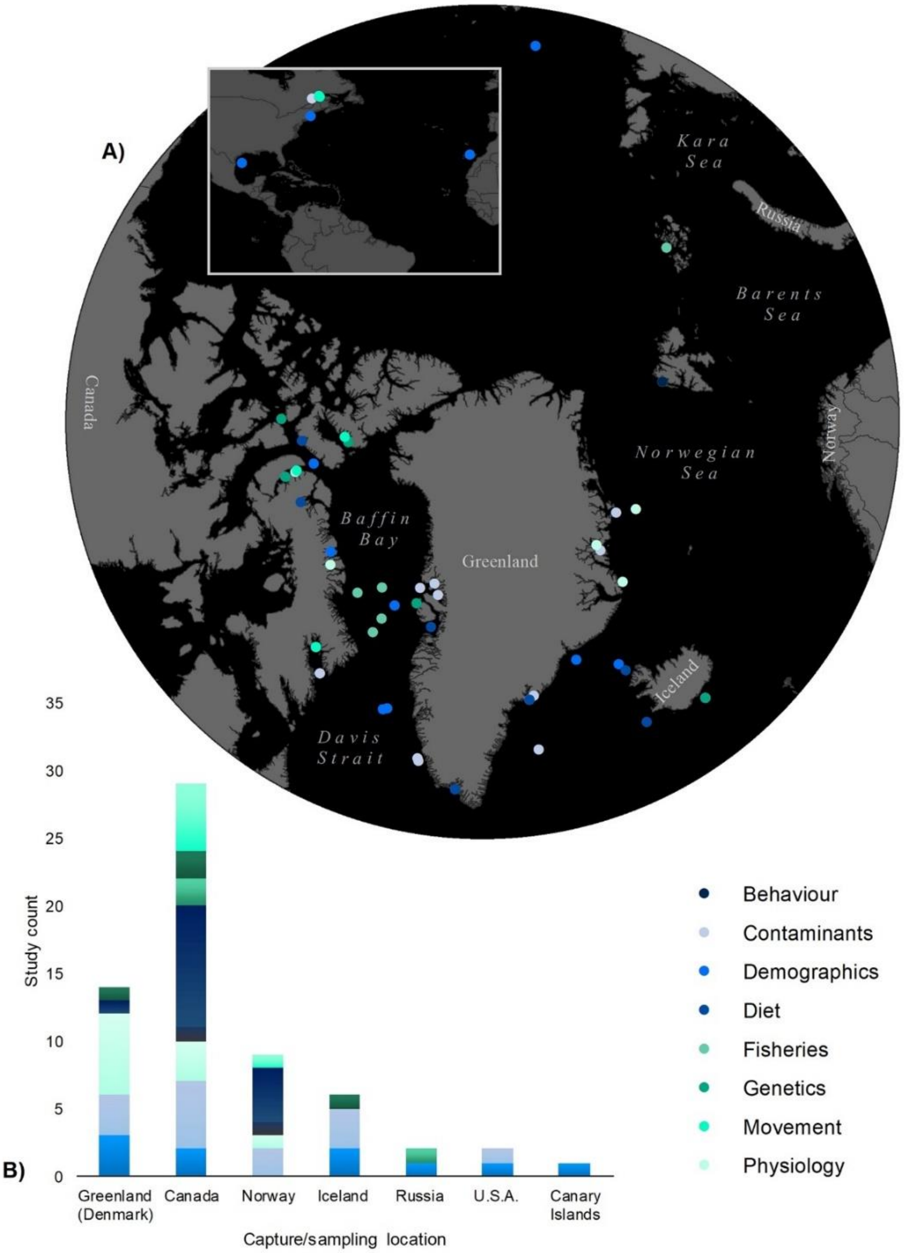

Figure 2.1 | Geographic coverage of Greenland shark studies by sampling location and research topic: A) Locations of Greenland shark capture/sampling (points represent sampling regions reported by each study, multiple points used for studies with several disparate sampling sites), B) Study count by country of Greenland shark capture/sampling and research focus (studies counted more than once where multiple sampled countries are reported).

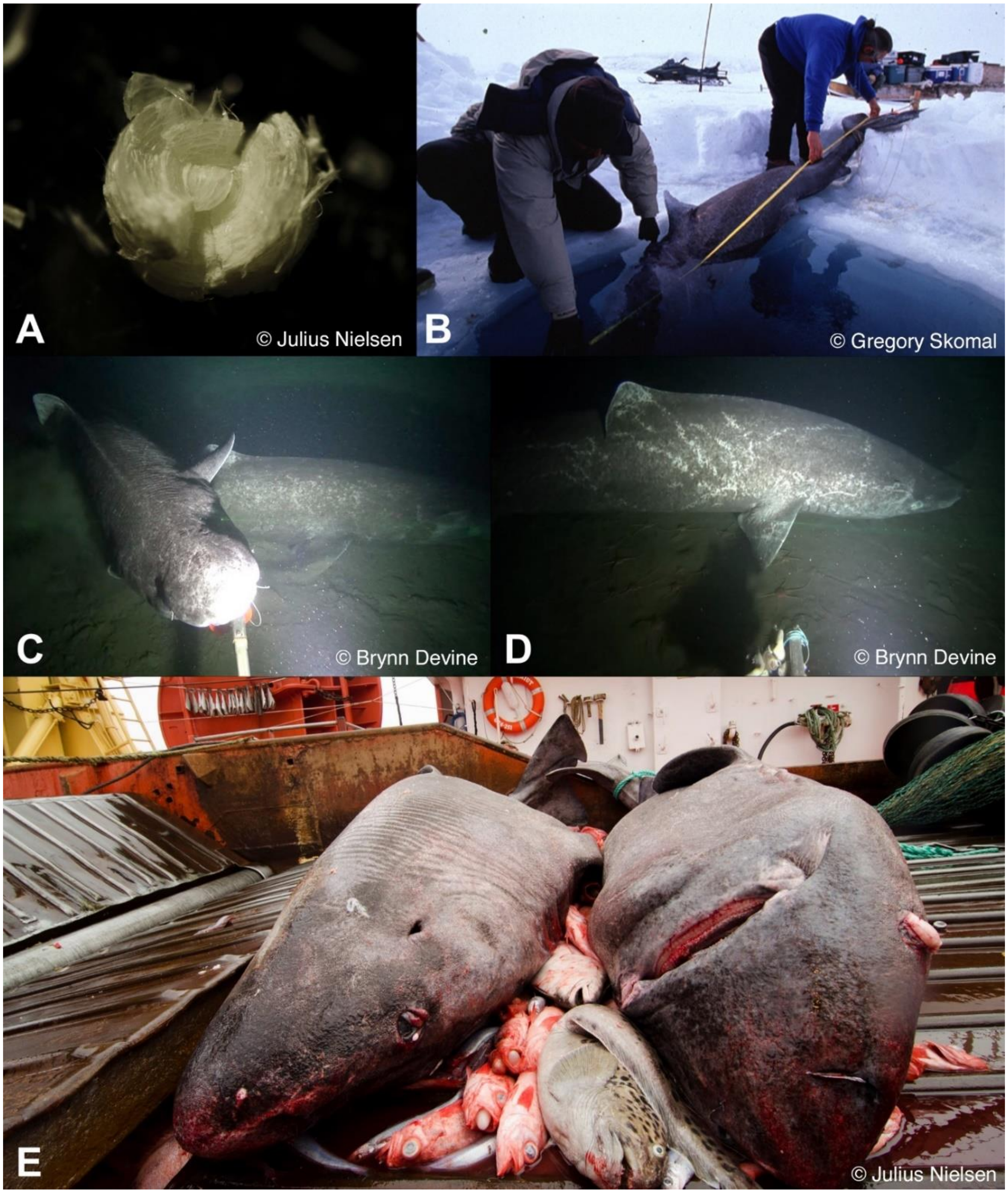

Figure 2.2 | Examples of Greenland shark demographics research. (A) Greenland shark eye lens for use in radiocarbon dating (photo © Julius Nielsen, used with permission). (B) Measuring the length of a Greenland shark captured through ice (photo © Gregory Skomal, used with permission). (C) Multiple Greenland sharks captured on BRUV footage (photo © Brynn Devine, used with permission). (D) BRUV image showing scar patterns used for identification of individual Greenland sharks (photo © Brynn Devine, used with permission). (E) Greenland sharks caught as bycatch in a fisheries trawl (photo © Julius Nielsen, used with permission).

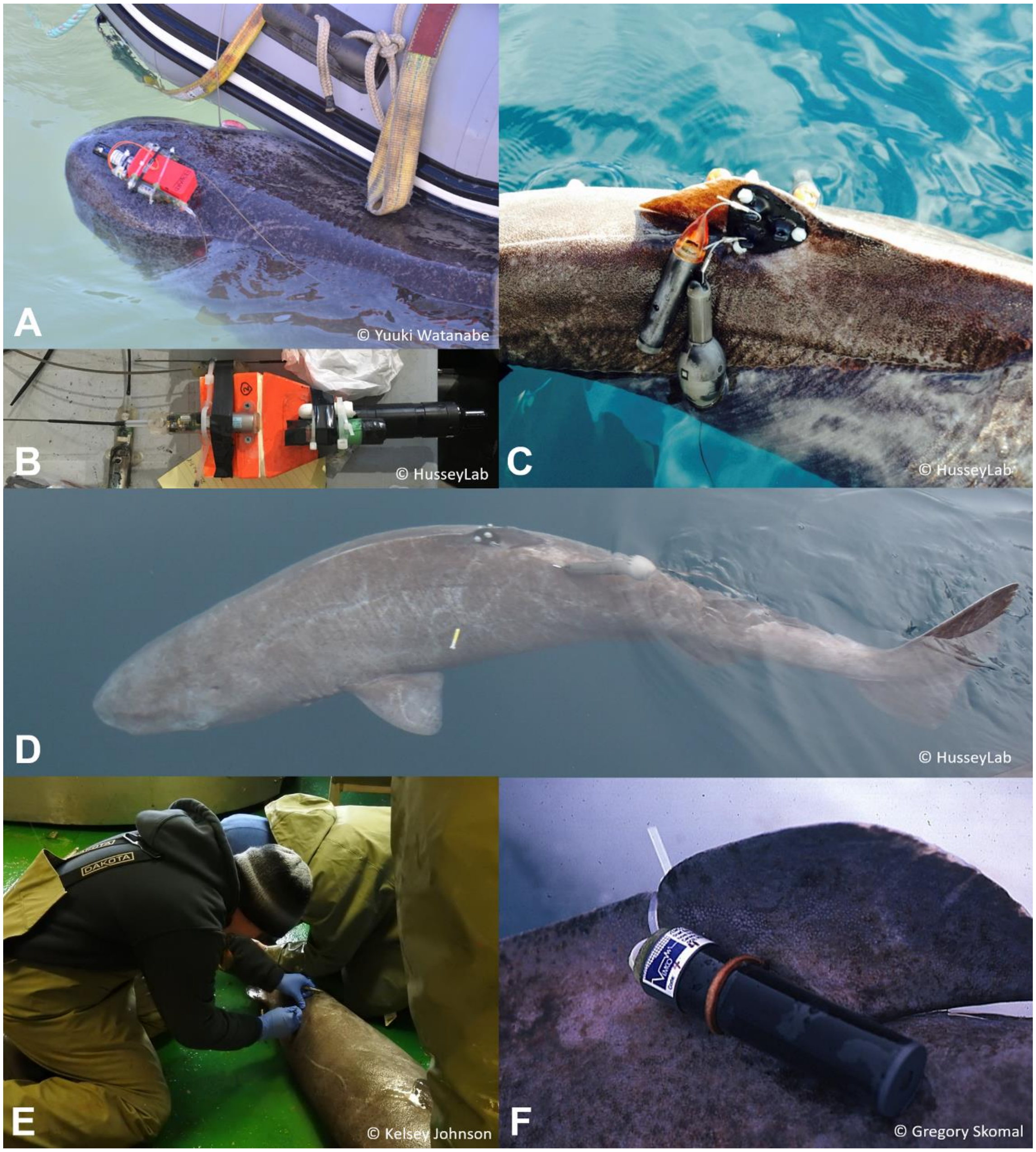

Figure 2.3 | Examples of Greenland shark movement studies: (A) A biologging package containing an accelerometer (Little Leonardo) mounted to the head (photo © Yuuki Watanabe, used with permission). (B) A biologging package containing a spot 6 tag (Wildlife Computers), a VHF tag, an accelerometer (Maritime Biologgers), and a CTD (Star Oddi) (photo © HusseyLab, used with permission). (C) An archival satellite tag and multiple mrPAT tags (Wildlife Comupters) mounted to the dorsal fin (photo © HusseyLab, used with permission). (D) A fin-mounted archival satellite tag (Wildlife Computers) and external marker tag (photo © HusseyLab, used with permission). (E) Internal implantation of an acoustic tag (VEMCO) for static acoustic tracking (photo © Kelsey Johnson, used with permission). (F) A dorsal fin-mounted acoustic tag (VEMCO) for mobile acoustic tracking (photo © Gregory Skomal, used with permission).

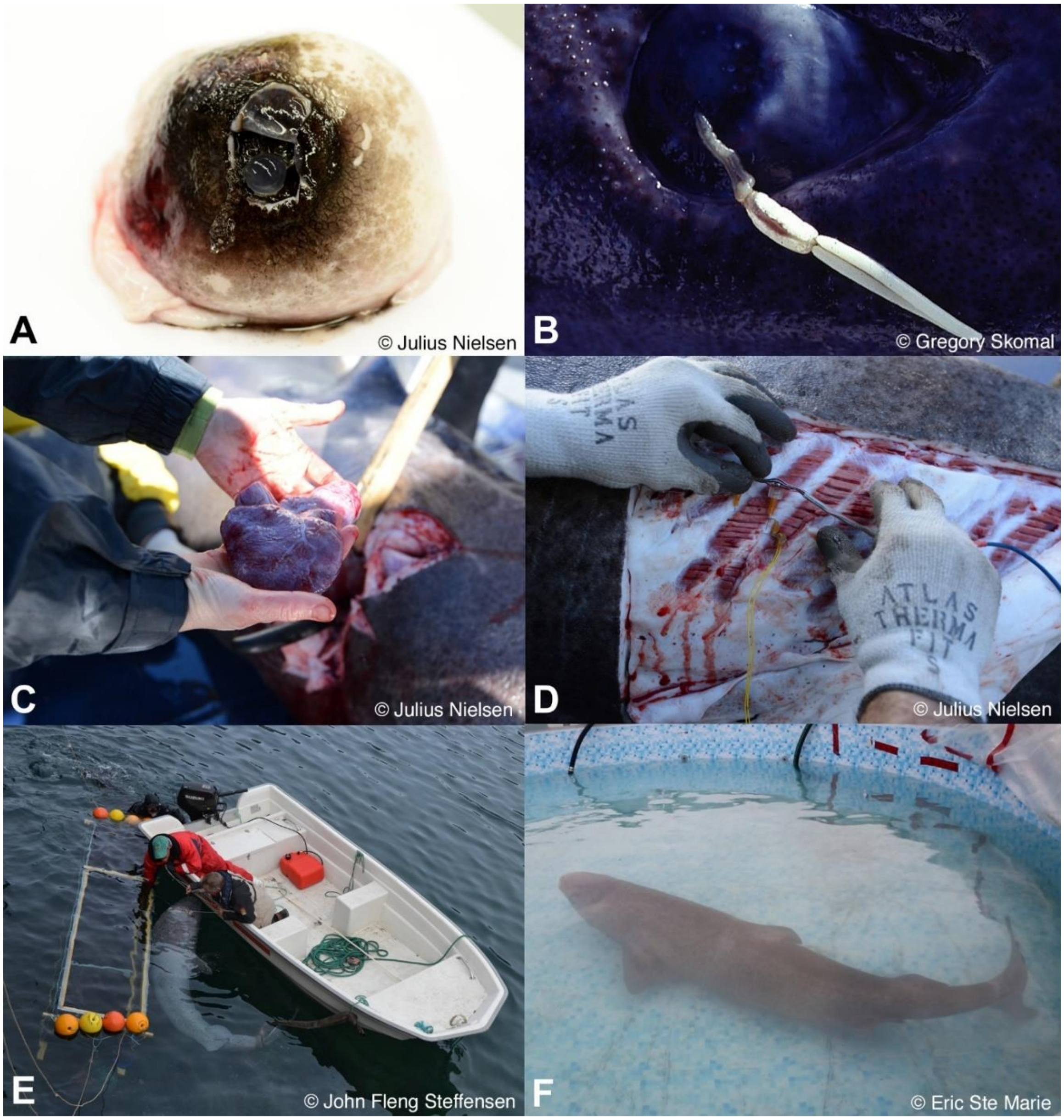

Figure 2.4 | Examples of Greenland shark physiological studies: (A) Eye with exposed cornea (photo © Julius Nielsen, used with permission). (B) Eye with parasitic copepod (O. elongata; photo © Gregory Skomal, used with permission). (C) Attachment of electrodes to heart (photo © Holly Shiels, used with permission). (D) Attachment of electrodes to the musculature (photo © Julius Nielsen, used with permission). (E) Shark and respirometry tank setup (photo © John Fleng Steffensen, used with permission). (F) Shark in respirometry swimming pool setup (photo © Eric Ste Marie, used with permission).

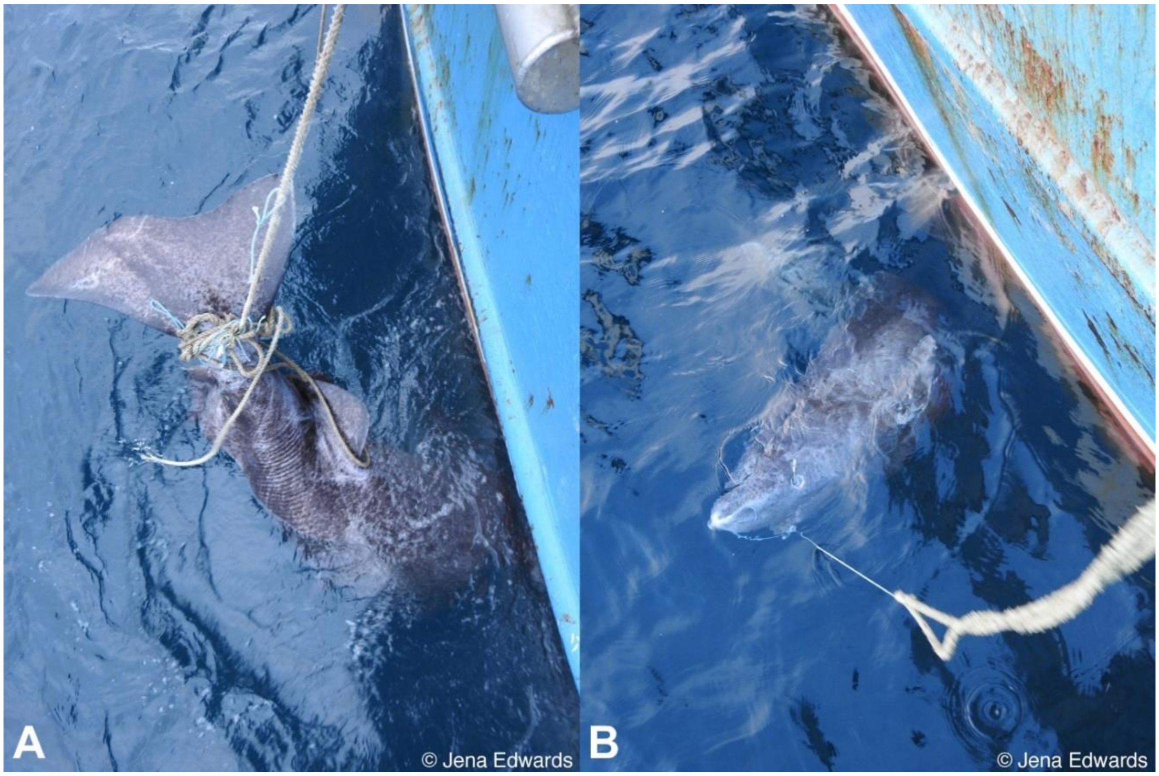

Figure 2.5 | Incidental capture of Greenland sharks via scientific bottom longline. (A) Shark entangled in mainline around caudle peduncle. (B) Shark hooked by mouth (photos © Jena Edwards).

Table 2.1 | An overview of current knowledge and data deficiencies in eight fields of Greenland shark (*S. microcephalus*) research, strategies to address data deficiencies, and potential actions to support management organization recommendations and Greenland shark conservation.

Research topic	Current knowledge	Knowledge gaps and limitations	Strategies to address data deficiencies	Potential actions to support management
Demographics and life history	Lifespan and age and size at maturity estimated. Local abundances at several sites in the Canadian Artic estimated. Potential juvenile habitats identified (Canadian and Russian Arctic).	**Stock assessment:** Population sizes, growth rates, mortality rates, sex ratios, and sustainable harvest levels unknown. A readily applicable and validated age determination method not available. **Reproduction:** Reproductive biology and ecology largely unknown.	**Stock assessment:** i. Develop routine ageing method ii. Ageing of individuals to determine age-at-length and inform population age structure. iii. Use BRUVs surveys to build a time series on which to estimate biomass and abundance indices (via a random sampling design, a consistent annual sampling regime, and a broad network of sampling sites). iv. Request detailed reporting of biological metrics (*e.g.* length, sex, and disposition) for bycaught sharks by fisheries observers. **Reproduction:** i. Use ultrasound techniques to identify pregnant females. ii. Electronic tags sutured into cloaca of pregnant females could help determine birthing time and location (as per Binder et al. 2014).	**Stock assessment:** i. Develop Harvest Strategy, including Harvest Control Rules (*e.g.* ICES Approach to Data-Limited Stocks). ii. Place video monitoring on fishing vessels to record presence/absence of claspers to estimate sex ratio. iii. Compare shark length measurements to age-at-length to estimate age class abundance/relative capture rates. **Reproduction:** Protect important mating/nursery areas and aggregation sites (upon identification).

Population genetics and genomics	Mitochondrial genome has been sequenced. Species phylogeny has been determined. Evolutionary history has been theorized.	Location of hybridization with *Somniosus pacificus* unknown. Generation times and genetic variability among individuals and populations unknown. Genetically determined susceptibility to environmental change unclear.	**Data collection:** Request at-sea observers to collect non-lethal tissue or parasite (iDNA) samples. **Define populations:** i. Use genetics to estimate generation times and effective population size (*e.g.* using half sibling approach). ii. Define genetically distinct populations/stocks. **Define range:** Examination of hybridization in southern regions (*e.g.* Gulf of Mexico) could extend the known range of Greenland sharks beyond the polar regions.	**Define populations and range:** Recommend appropriate size and location of management boundaries.

Movement ecology	**Seasonal movements:** i. Horizontal tracking shows long-distance timed/directed migrations. ii. Observed occurrence in shallower waters with increasing latitude. iii. Visual records of philopatry observed in St. Lawrence Estuary (unpubl. data). **Vertical movements:** i. Records of movement in shallow water and mid water column under ice and in estuarine waters and (acoustic and pop-off satellite tracking). ii. Vertical movements appear to be associated with light cycle in shallow water.	**Seasonal movements:** i. Lack of long-term (*i.e.* multi-year) records showing seasonal/annual movements. **Vertical movements:** Limited records of detailed vertical movement behaviours available (*e.g.* early depth and temperature records binned at 60sec-6hr intervals). **Distribution:** Short-term monitoring insufficient to capture complete range of movements.	**Seasonal movements:** Increase monitoring duration using long-term passive acoustic, archival, or satellite methods and improved technologies (*e.g.* extended battery life, depth ratings, etc.). **Vertical movements:** i. Use high-resolution time-series data to create continuous movement tracks. ii. Create state-space models to decompose dives and associate oscillatory patterns with discrete behavioural types (*e.g.* post-release recovery). iii. Compare overlap in vertical distribution with that of fisheries target species. **Distribution:** Use large-scale passive acoustic infrastructure and long-term satellite telemetry approaches to define range and identify mating/pupping grounds.	**Seasonal movements:** i. Potential seasonal closures for human activities in annual high use areas to minimize negative impacts to Greenland shark populations. ii. Dynamic Area Management to protect unexpected aggregations. **Vertical movements:** Inform fish harvesters of shark behaviour patterns to facilitate efforts to minimize shark catch (e.g. set gear at depths and times of day when sharks tend not to be present). **Distribution:** Bilateral or multi-lateral agreements between nations or via Regional Fisheries Management Organizations (RFMOs) to conduct science and manage species on a population level.
Behaviour and interactions	**Capture and release:** Preliminary tagging studies have examined post-release behaviour and survival rates following experimental capture. **Foraging behaviour:** i. Indirect evidence of live predation on seals. ii. Slow swim speeds relative to body size but high roll acceleration. iii. Direct observations of scavenging. iv. Aggregation behaviour observed.	**Capture and release:** Post-release survival rates require further study (currently insufficient for adjusting mortality factors in a population model). **Foraging behaviour:** i. Tactics of prey capture unknown (a cryptic predation approach hypothesized). ii. Nature and frequency of intra- and interspecific interactions unknown.	**Foraging behaviour:** i. Use cameras (still and video) deployed on various platforms (*e.g.* animals, Remote Opeated Vehicles, fishing gear, cables) to observe foraging behaviour directly. ii. Use animal-borne hydrophones (sample soundscape) to assess interactions with vocalizing animals (e.g. marine mammals). iii. Use of VMTs (acoustic transponders) to examine intra- and inter-specific interactions.	**Capture and release:** Develop and promote safe handling practices for the release of sharks caught as bycatch. **Foraging behaviour:** Use understanding of feeding modes (*e.g.* suction feeding) and preferences to inform gear modifications, gear deployment, and bait use.

Physiological adaptations	**Physiology:** i. Exhibit extreme longevity (estimated between 272-512 yrs). ii. High antioxidant enzyme levels and low blood O_2 affinity recorded. **Sensory abilities:** i. Olfactory organs highly developed, consistent with benthic predator/scavenger lifestyle. ii. High incidence of blindness due to eye parasitism (except in the St. Lawrence River). iii. Observations of vision-dependant behaviours suggest ability to undertake active predation.	**Physiology:** ii. Maximum reserve density suggests lifespan may currently be underestimated. ii. Sensitivity to environmental shifts unknown. ii. Details of heart function unknown (may play a role in longevity). **Metabolic rate:** i. Metabolic rate and rate of O2 consumption unknown. ii. Potential link between hemoglobin properties and cold-tolerance. iii. Potential links between high antioxidant enzyme levels and cold tolerance, deep diving behaviour, and longevity. **Sensory abilities:** Importance of vision relative to other senses unknown.	**Metabolic rate:** i. Measure oxygen consumption and determine metabolic rate using containment approaches. ii. Use metabolic rate to determine energetic requirements; possible extrapolation to necessary frequency of feeding using a bioenergetics approach. **Sensory abilities:** Further examination of sensory systems and brain morphology required (*e.g.* via sampling of experimental and/or commercial bycatch mortalities).	**Metabolic rate:** Individual energy requirements could inform population-level requirements (*i.e.* biomass required to sustain population) – could provide considerations for Total Allowable Catch of prey species. **Sensory abilities:** Inform development of shark deterrents for fishing gear; make gear more noticeable to sharks (e.g. pingers, scent, electronic waves).
Diet and trophic ecology	**Diet:** Benthic and pelagic feeding from predominantly offshore teleost sources suggested. **Ecological role:** Greenland sharks are likely important predators and likely occupy a high trophic position.	**Diet:** Possibility for sub-population dietary specialization unknown. **Ecological role:** i. Effect of consumption by Greenland sharks on prey populations unknown. ii. Role in food web stabilization and connectivity unknown. iii. Role of longevity nutrient/energy transfer in food webs over time and space uncertain.	**Diet:** i. Collect sample tissues (muscle, blood plasma) by non-lethal methods to examine diet. **Ecological role:** i. Measure metabolic and consumption rates in situ. ii. Further refine Arctic marine food web structure and quantify energy flow and trophic transfer efficiencies. iii. Use EcoSim models to examine the potential trophic effects of Greenland shark population increases and decreases.	**Ecological role:** i. Enhance understanding of Greenland sharks and their ecological role by stakeholders and general public. ii. Determine sustainable harvest levels which are predicted to maintain ecosystem function.

Table 2.2 | Research goals and considerations for advancing the study of long-lived species.

Research goal	Potential methods and considerations for long-lived species
Visual identification of individuals for demographic studies	Scar patterns and external markings may be used to identify individuals over short time periods (Devine 2018), but these may also change or disappear with age (Robbins & Fox 2013). External markers (*e.g.* Floy tags) facilitate identification (Section 1), however, studies should determine the average duration of tag retention by target species.
Determining population conservation parameters	While genetic markers allow estimation of effective population sizes (N_e) the application of this approach for conservation purposes requires generation time and a species-specific mutation rate to be accurately defined (Section 2). For species that cannot easily be aged, it is difficult to accurately determine generation times and mutation rates. The use of evolutionarily significant units (*sensu* Frasier & Bernatchez 2001), should be explored as an alternative.
Monitoring behaviour over time	For species whose movements cover large distances over extended time periods, it is important that the duration of monitoring (limited by tag lifespan and duration of retention) reflects the temporal scale of the observed behaviours. Improvements to electronic tag design (*e.g.* increased battery life), or the use of multi-tag approaches (Hussey et al. 2018) will extend monitoring durations and can record behaviours occurring over extended timespans (Section 3).
Understanding ontogenetic shifts in sensory capabilities and behaviour	In fishes, ontogenetic changes in the brain and neuroanatomy may affect the relative importance of senses such as vision and olfaction and may, in turn, be associated with age-related alterations in diet, habitat use, and activity patterns (Lisney et al. 2017). Examinations of brain morphology and behavioural studies should target animals from a broad range of age-classes to understand the influence of ontogeny on shifts in the ecological role of individuals over centuries of longevity.
Determining the physiology of extreme longevity	Measurements of metabolic rate (*i.e.* using oxygen consumption as proxy), blood oxygen consumption, and the cardiovascular system (see Section 5) could provide insight into the physiological mechanisms of longevity.
Examining trophic relationships and connectivity	Extreme longevity may play a role in the ability of mobile predators to connect and stabilize food webs (*e.g.* by extending the number of migrations and feeding events that can occur over an animal's lifespan). Similarly, an understanding of the ecological footprints of long-lived individuals may improve the accuracy of predictive ecosystem models (*e.g.* EcoSim).

CHAPTER 3

Thinking deeper: Uncovering the mysteries of animal movement in the deep sea

3.1 Introduction

The deep ocean, defined as all marine waters exceeding 200m depth (Armstrong et al., 2012), comprises approximately 90% of Earth's ocean surface area (Gage and Tyler, 1992) and provides the largest living space on Earth (Uiblein et al., 2003; Ramirez-Llodra et al., 2010). Nevertheless, the deep sea remains the least explored of all terrestrial or aquatic ecosystems (Ramirez-Llodra et al., 2010). Despite the discovery of new habitats such as hydrothermal vents, cold seeps, and cold-water reefs, remote exploration has covered a mere 5% of the area encompassed by the deep sea to date, and less than 0.01% has been subject to thorough biological investigation (UNEP, 2007; Ramirez-Llodra et al., 2010; Benn et al., 2010). This research has shown that despite environmental constraints (*e.g.,* a lack of sunlight, extreme temperatures and ambient pressures, and low resource availability), many deep-water ecosystems contain diverse and highly specialized communities (Gage and Tyler, 1992; Ramirez-Llodra et al., 2010). Importantly, these ecosystems likely harbour the largest number of unidentified species, those that are imperiled (*e.g.,* some deep-water corals; Eytan et al., 2009), and commercially important species that have already seen increases in exploitation (Branch, 2001; Hussey et al., 2017). *K*-selected life history characteristics shared by most deep-living species, including slow growth and metabolic rates, late age at maturity, and low fecundity, are thought to render this group of species particularly vulnerable to fisheries exploitation and other anthropogenic impacts (*e.g.,* deep-water sharks; Kyne and Simpfendorfer, 2007; Rodríguez-Cabello and Sánchez, 2014; Brooks et al., 2015;

Shipley, 2017). It has even been suggested that slow progress in the advancement of deep-ocean studies may have led to once viable stocks becoming commercially extinct before they could even be properly documented (Haedrich et al., 2001). In addition to the expansion of fisheries into deeper offshore waters (Morato et al., 2006), growing interest in the exploitation of abiotic resources such as valuable mineral deposits (Hoagland et al., 2010) is promoting a rise in technological innovations that are allowing the investigation of the deep sea to occur at an unprecedented rate (UNEP, 2007).

In recent years, technological developments in animal tracking (*i.e.*, biotelemetry) have allowed animals to be equipped with electronic tags that collect, archive, and transmit a diverse range of data (Cooke et al., 2004; Hussey et al., 2015). These tags are revolutionizing our understanding of the scales of aquatic animal movements in both time and space (Bonfil et al., 2005; Block et al., 2011), revealing the physiological costs associated with movement and migration (Hinch and Rand, 1998; Hinch and Bratty, 2000), how environment shapes movement decisions (Peklova et al., 2012; Thums et al., 2012; Hazen et al., 2013) and inter-individual differences in movement decision making (Cooke et al., 2005; Campana et al., 2015), to name but a few examples. As a result, biotelemetry is now broadly accepted by scientific and resource manager stakeholders as a method for examining the movement ecology of wild organisms, with data now directly influencing management at various levels (Brooks et al., 2018; Crossin et al., 2017; Barton et al., 2015; Cooke et al., 2012). While electronic tracking provides a practical approach to explore the movement behaviours of a wide range of species across life history stages (Hawkes et al., 2017), and nearly all aquatic ecosystems (marine, estuarine, and freshwater) (Cooke et al., 2013; Hussey et al., 2015), certain environments (*e.g.*, the deep ocean) pose logistical complications, and therefore remain largely understudied. The monitoring of deep-water species adds additional layers of complexity in gear design and animal health protocols. As such, deep-water biotelemetry is rarely used. This bias is clearly reflected in the telemetry equipment available to monitor deep-water species, with most commercially available acoustic receivers, for example, rated to a maximum depth of only 500 m.

Despite spending significant periods of time in shallow water, many marine animals including numerous whales (*e.g.*, beaked whales, *Mesoplodon densirostris, Ziphius cavirostris*; Tyack et al., 2006; Baird et al., 2008), teleost fishes (*e.g.*, silver eel, *Anguilla anguilla L.*; Tesch 1989), and elasmobranchs (*e.g.,* bigeye thresher, *Alopias superciliosus*; Nakano et al., 2003; Weng and Block, 2004) are known to undertake frequent vertical movements to bathyal depths. Telemetry studies on these and other deep-diving species have provided valuable insight into the connectivity of shallow and deep-water ecosystems (Thorrold et al., 2014), physiological adaptations allowing recurrent animal movements across intense environmental gradients (i.e., temperature and pressure; Croll et al., 1992; Castellini et al., 1992) as well as novel records of extreme diving behaviour in surface-associated species (*e.g.*, the leatherback sea turtle, *Dermochelys coriace*, Eckert and Eckert et al., 1989; elephant seal, *Mirounga angustirostris*, DeLong and Stewart, 1991; and bottlenose whale, *Hyperoodon ampullatus*, Hooker and Baird, 1999). However, in contrast to species that spend most or all of their lives at depth, the inevitable return of air-breathing or vertically migrating species to shallow water eliminates some of the unique challenges associated with accessing and monitoring the movements of exclusively deep-water species.

There is a pressing need for deep-sea research techniques to advance beyond their current limitations, however, given current exploitation rates, the rate of technological development to allow this is currently insufficient. This study aims to address this issue by presenting a systematic review of the literature on deep-water telemetry, summarizing our current knowledge and examining the application of tracking technologies that have revealed key insights into the movement of deep-sea species thus far. We also address several challenges that have impeded deep-sea telemetry to date, including constraints on the deployment, recovery, and long-term functionality of telemetry equipment at extreme depths, the inaccessibility of deep-water habitats and focal species, and risks to the survivability of animals that are brought to the surface and returned to deep water (Sigurdsson et al., 2006; Hannah et al., 2008; Rankin et al., 2017). To prioritize the distinct nature of these challenges, and the highly specialized technologies and approaches required to overcome them, only studies where monitoring primarily took place at or below 200m depth were included in these analyses. Studies focusing on species exhibiting deep-diving behaviour, but which are otherwise associated with the photic zone (*e.g.,* basking sharks, *Cetorhinus maximus*, Sims et al., 2003; and whale sharks, *Rhincodon typus,* Graham et al., 2006), were therefore not included. By providing examples of research that has overcome the difficulties of working with deep-water species (*i.e.,* those that spend most or all of their time at 200m depth or greater), this review provides a baseline for current and future deep-sea research, while emphasizing the pressing need for the expansion of deep-sea telemetry and for the development of improved technologies to facilitate it.

3.2 Methods

To identify all relevant deep-water biotelemetry articles, electronic database searches were conducted using the following search engines: JSTOR, Web of Science, Google Scholar, Novanet, ScienceDirect and SpringerLink Journals, Elsevier, and Nature. Studies were found using the keywords: ‘deep water telemetry’, ‘deep sea acoustic tracking’, ‘abyssal acoustic telemetry’, ‘deep sea telemetry’, ‘acoustic tracking’, and ‘archival tag deep water’. In addition, works cited in papers found during these electronic searches, but not identified directly by the search, were also used. All studies focusing on deep-water telemetry and published by April 1st, 2018 were included.

Studies were first categorized into three groups based on the use of acoustic (**Table 3.1**), satellite (**Table 3.2**), or archival telemetry (**Table 3.3**), as determined by tag type (see Section 3.1). Data from all categories were extracted and compiled into three data sheets corresponding to these respective telemetry study classes (see **Table 3.4** for definitions of extracted data categories).

3.3 Results and discussion

A global total of 48 deep-water biotelemetry studies were identified for the period 1986–2018 (**Figs. 3.1 and 3.2**), of which 22 were focused on acoustic telemetry (**Table 3.1**), 23 on satellite telemetry (**Table 3.2**), and 3 on archival tag data (**Table 3.3**). For one satellite telemetry study (Seitz et al., 2003), archival data from two recovered satellite tags were analysed and published independently, warranting its inclusion in the archival study list (Seitz et al., 2005; **Table 3.3**). A further study is listed along with both the satellite and archival studies (**Tables 3.2, 3.3**, respectively), as both tag types were deployed simultaneously, and analyses were reported together (Loher et al., 2011). Global patterns in the locations of deep-water telemetry studies showed a strong bias toward northern Atlantic and Pacific waters, with only one satellite and two acoustic telemetry studies (6% of total) occurring in the southern hemisphere (Hissmann et al., 2000; Brown et al., 2013; Daley et al., 2015) (**Fig. 3.1**, see Section 3.4.2 for further discussion).

3.3.1 Electronic tracking methods

3.3.1.1 Acoustic telemetry

Acoustic tracking can be categorized as either mobile or static, with each method varying by the equipment and approach used. During mobile tracking, researchers use a tracking vessel to maintain close proximity to a tagged animal and the GPS position of the ship is assumed to be the same as that of the tagged fish, thereby allowing the observation of fine-scale localized movements. Static acoustic tracking employs moored acoustic receivers that record and archive transmissions from tags in animals that pass within the detection range of a receiver (Heupel et al., 2006). The terms ‘active’ and ‘passive’ have been used by some authors to describe mobile and static acoustic tracking respectively (Heupel et al., 2006; Simpfendorfer et al., 2010; Marshell et al., 2011; Afonso et al., 2014). However, the term ‘passive’ has long been used for both mobile and fixed sonar systems that emit no signals (*e.g.*, detecting mammal sounds) and the term ‘active’ for sonars that emit signals (*e.g.*, echosounders) (Maranda, 2008). Henceforth we recommend the use of the terms ‘mobile’ and ‘static’ to avoid confusion, especially since active sonars can be used on fixed stations to track fish with transponders and passive sonars on mobile stations to track acoustic pingers.

Mobile acoustic tracking of deep-water species is largely limited by the use of surface-based receivers where detection ranges are typically less than the distance between the surface and the desired monitoring depth of the focal species. In contrast, advances in static acoustic telemetry have reduced physical labour requirements, expanded the number of individuals and species that can be monitored simultaneously, and significantly increased tracking durations relative to mobile tracking studies. These factors have likely contributed to the greater use of static tracking relative to mobile acoustic tracking in the reviewed studies (Kessel et al., 2014). Of the 22 acoustic telemetry studies, only two used mobile acoustic telemetry and onboard receivers (Hissmann et al., 2000; Afonso et al., 2014). Animals in these studies were outfitted with VEMCO (VEMCO Ltd., Halifax, Nova Scotia) acoustic transmitters, including pressure sensors (V16P-4HI, Hissmann et al., 2000; β-V13P-1H, Afonso et al., 2014) that provided records of vertical as well as horizontal movements.

The majority of examined acoustic tracking studies employed static acoustic telemetry (**Table 3.1**). In most cases, these studies adopted Priede and Smith's (1986) approach, using free-fall vehicles (FFVs) or unmanned platforms such as AUDOS (Aberdeen University Deep Ocean Submersible) to remotely observe and track the movements of free-swimming abyssal fishes at depths far exceeding the ratings of traditional acoustic receivers. These autonomous monitoring platforms were composed of metal tubular framework and equipped with a variety of equipment including downward-facing cameras, baited acoustic transmitters, and some version of the ATEX (Acoustic Tracking Experiment, *e.g.,* Scanning ATEX, Transponding ATEX) receiver system (Fig. 4a,b). FFVs were typically deployed over the stern of a ship and descended by free-fall to a position buoyed just above the seabed where they would remain anchored by a ballast for a maximum interval of 24 h. During the deployment period, abyssal fishes attracted by the odour of the baited platform would be enticed into ingesting bait-wrapped transmitters tied within the centre of the field of view of the camera. Following tag ingestion, fish movements could be monitored within the detection range of the FFV's receiver system until either the transmitter was shed by regurgitation or passage through the gut, or the tagged fish moved beyond the extent of receiver's detection radius. Meanwhile, cameras mounted to the unmanned platform could collect additional data such as the abundance and diversity of species attracted to the FFV, as well as their arrival and departure times from the platform's vicinity. After reaching the end of a pre-determined monitoring period, an acoustic time release command would remotely release the buoyant vehicle from its ballast, returning the FFV and its associated equipment (apart from any ingested transmitters) to the surface for collection.

Unlike VEMCO manufactured receivers which detect only the presence of tagged fish within the receiver's detection radius, AUDOS receivers also allowed inferences of the distance and position of the animal around the platform (Priede and Bagley, 2000). This was initially accomplished by measuring the received signal strength of ingested tags (Deep Ocean pingers) using the ATEX receiver system. Through further development, Deep Ocean pingers were eventually replaced by Code Activated Transponders (CAT), and the first stage of the custom-built ATEX receiver was also upgraded to an active array to allow range and bearing to be measured more accurately. In these later deployments, detection range was calculated using the travel time of an active transmission pulse emitted by a CAT to the detection of the received pulse at the AUDOS platform using the TRATEX receiver system.

CATs developed for these studies were also custom-built with consideration of the extreme pressures experienced at depths beyond 4000m and could be detected to a maximum distance of 1000m from the AUDOS (Bagley and Priede, 1997; Priede and Bagley, 2000). In contrast to modern VEMCO transmitters which have a solid housing, CATs had a flexible seal to allow volume changes to occur and the electronics and battery were immersed in oil, allowing internal components to experience ambient pressures (Priede and Bagley, 2000). Vent holes were also drilled in the tops of lithium batteries to equalize pressure and avoid deformation of the casing and internal short-circuiting; however, this practice is considered unsafe and may not be efficient for mass tag production (Bagley et al., 1999; Priede and Bagley, 2000). Unlike most contemporary acoustic transmitters, which transmit acoustic signals at timed intervals, CATs remained in a ‘sleep state’ until activated by two sequential pulse codes transmitted by the sonar system, after which a return pulse was emitted to denote the location of the tag (Bagley and Priede, 1997). By varying the nominal delay of activation pulses corresponding to each deployed CAT, individual tagged fish could be identified and tracked (Bagley and Priede, 1997).

Transmitters used in the remaining static acoustic studies were VEMCO manufactured (V13SC-1H, Afonso et al., 2012; V9SC-2L, Afonso et al., 2012; β-V13P-1H, Afonso et al., 2014; V16-4H, Daley et al., 2015; V16-6H, V16-5H, V16-4H and V13–1L, Hussey et al., 2017; Barkley et al., 2018; V16P-4HI,P- V3–6H, V3–4H,HI, V3-6H, V3-4H, Hissmann et al., 2000), with the majority belonging to the product line of 69 kHz tags (ranging in size from 21mm to 98mm length and weighing between 1.6g – 17.3 g; VEMCO product specifications, https://vemco.com); likely due to the more restricted detection range of smaller and less powerful 180 kHz tags. One study also used VEMCO-manufactured pingers (continuously transmitting tags, 60–65 kHz) to facilitate mobile acoustic tracking (Hissmann et al., 2000).

Recent static acoustic studies have used VR2 series VEMCO receivers (VR2W, VR2-AR, VR2-TX) (Afonso, 2012, Afonso et al., 2014; Weng, 2013; Daley et al., 2015; Hussey et al., 2017). These receivers detect tags transmitting at 69 kHz and 180 kHz and have a maximum rated depth of 500m (VEMCO product specifications, https://vemco.com). In two cases, however, VR2 receivers were deployed at depths exceeding this rating (Daley et al., 2015; Hussey et al., 2017) and were shown to remain functional at depths down to 1011m (Hussey et al., 2017, see below).

The maximum range of detection of acoustic transmitters can vary considerably owing to varying oceanographic and weather conditions as well as vessel noise and behaviour at sea. Determination of maximum detection range was only reported in three of the reviewed acoustic telemetry studies which employed VEMCO equipment. In one study, a series of range tests were conducted using three transmitter models (VEMCO V9, V13, V16) with tags either set on a hanging mooring at a distance of 300m from a receiver station and 50m above the bottom (~150m depth) or hung from a vessel (at 150m depth) which was left to drift for 2000m while passing over the station (Afonso et al., 2012). These tests provided absolute maximum detection ranges between 877 and 963m across the three tag models, however, mean distances for transmission detection rates of 50% were much shorter and varied depending on the time of day (500–600m during the day, 100m at night) (Afonso et al., 2012). The second study, which used a transmitter towed behind a vessel at the study site, found the maximum detection radius to be 900m and reported a 95% transmission detection rate within a radius up to 650m (Daley et al., 2015). Finally, a year-long range test was conducted in the Eastern Canadian Arctic where test transmitters (V16, V13, and V9) were deployed on deep-water moorings (at depths between 1020 and 1063 m) to determine the detection range of VEMCO VR2W receivers at unprecedented depths down to 879m (Hussey et al., 2017; Appendix S1).

3.3.1.2 Satellite and archival telemetry

Pop-up Satellite Archival Transmitters (PATs or PSATs) are generally attached to animals externally by a dart or anchor from which the tag is programmed to release after a pre-determined time interval. Upon release, the tag is buoyed to the surface where the antenna is exposed to air and the stored data is transmitted to the Argos satellite system (Campana et al., 2015). These tags can measure the large-scale movements or migrations of marine organisms while simultaneously archiving environmental data including, depth (measured in units of pressure), ambient light (sometimes used for geolocation estimates), and ambient temperature (also modelled for geolocation). By employing the Argos satellite system, data can be globally transmitted and received without requiring tag retrieval.

PATs used in the study of deep-water species were manufactured by Wildlife Computers (Redmond, WA, USA), Lotek Wireless (St John's, NL, Canada), and Microwave Telemetry (Columbia, MD, USA; Table 2). Most studies used tag models produced by Wildlife Computers (*e.g.,* Mk9, Mk10, and miniPAT). However, one study deployed HR X-tags manufactured by Microwave Telemetry which have a high sampling rate (~133-second resolution), but a limited lifespan (14 days) (Shipley et al., 2017). Maximum tag deployment lifespans ranged from 40 d (Peklova, 2012) to 3 years (Loher, 2011) as dictated by battery life or memory capacity/resolution of data collection. Deployed PAT and archival tags also contained a variety of environmental sensors programmed to record and archive ambient temperature and light data, salinity and dissolved oxygen, as well as depth (ambient pressure). Sampling intervals for depth, temperature, and light intensity ranged from 1 to 240 s, with depth and temperature sampled more frequently than light intensity. Depth data were typically recorded at a resolution of 0.5m (± 1% accuracy,± 2 resolutions; Loher and Seitz, 2006; Brown et al., 2013; Rodríguez-Cabello et al., 2014, 2016) and 4m (Seitz et al., 2003; Loher and Blood, 2009; Loher and Clark 2009), while temperature data were reported at resolutions of 0.05°C (Brown et al., 2013; Loher and Seitz, 2006) and 0.1°C (Seitz et al., 2003; Loher and Blood, 2009; Loher and Clark, 2009). Due to limitations on the size of data transmissions allowed by the ARGOS message format and tag processing capability for older models, approximately half of these studies used built-in tag software to compress environmental and depth data into user-specified bins that typically summarized data collected over 6 h (Brown et al., 2013; Campana et al., 2015) or 12 h intervals (Seitz et al., 2003, 2007, 2011; Loher and Seitz, 2008). In contrast, high-resolution time-series data were reported by only a few studies where tags were programmed to record depth and temperature at high sampling rates (Shipley et al., 2017; Peklova, 2012) or where physical tag retrieval allowed access to archived tag data (Seitz et al., 2003, 2011; Loher et al., 2008).

One deep-water study employing satellite tags also incorporated model LTD1300 long-term archival tags (Lotek Wireless, 0.5m resolution depth records at 1 min intervals, tag life ≤5yrs) and is therefore listed in both the satellite and archival telemetry categories (Loher, 2011; **Tables 3.2 and 3.3**). A second archival study used the archived data obtained from two recaptured satellite tags which were also described in one of the listed satellite studies (Seitz et al., 2005, Table 3; from Seitz et al., 2003 deployments, **Table 3.2**). This study then used minute-by-minute depth records (4m resolution) only available in the archived tag data to examine vertical movements associated with Pacific halibut spawning. The final archival study used DST milli (Star-Oddi) tags programmed to record temperature (-1 °C to +40 °C) and pressure (0.5–900 m) every 10, 15, or 60 min for up to 1 year (battery life) or 21738 recordings (memory capacity; Boje et al., 2014).

All deployed PAT models were rated to depths down to 2000 m, however, depth-dependent programming of the integrated 1800m tag release device (RD1800) often reduced the maximum depth of monitoring. Programmed tag release devices are typically set by the researcher to occur after a predetermined interval following the deployment date (*e.g.,* 1 or 6 months). However, tag releases can also be coded by the researcher to activate if no change in depth is detected over a chosen time interval, presumably due to the death of the animal or tag dislodgement, or if the sensors detect depths approaching the tag's maximum rating. The programmed release setting can result in the premature release of a tag if the target animal leads a highly sedentary lifestyle, or if they occupy extreme depths (> 2000 m), as many deep-water species do. For inactive species, such as Greenland halibut and Arctic skate, the option for tag release with constant depth was disabled (Peklova, 2012). In the case of animals whose movements exceed maximum tag depth ratings, resolving this problem is not quite so simple. For example, in one study, five Mk10 PAT tags prematurely released from their host Patagonian toothfish (*Dissostichus eleginoides*); two of which released on the day following tagging when fish moved to depths beyond 1800m (Brown et al., 2013). Similarly, RD1800-induced premature tag releases were reported following the deep-water excursions of tagged leafscale gulper sharks (*Centrophorus squamosus*; Rodríguez-Cabello and Sánchez, 2014). For the prevention of tag damage and the loss of archived data, deactivation or removal of this mechanism is not advisable for tags used on species expected to occupy deeper waters. Instead, innovations in tag design are needed to increase tag depth ratings (see Section 3.7.4).

3.3.2 Study species, locations, and tagging success rates

3.3.2.1 Acoustic telemetry study statistics

Since 1986, 13 species of chondrichthyan and teleost fishes (2 and 10 respectively) have been monitored to depths of nearly 6000m (**Fig. 3.2**), with over 780 individuals tagged (**Table 3.1**).

Most of these studies (n=13, 59% of acoustic studies) collected movement data on members of the genus *Coryphaenoides* using high-tech free-fall vehicles to reach unprecedented (and unrepeated) depths for animal tracking (maximum 5900m depth; see Section 3.2.1; **Fig. 3.2**). While these studies were relatively limited in tracking duration (1–24 h) due to the nature of tag attachment (via tag ingestion) and were restricted to the detection radius of a single receiver platform (500–800 m), a sophisticated hydrophone system allowed the highly precise monitoring of fish movements within the field of detection (**Fig. 3.3d**). These systems were first designed to monitor the assumed "sit-and-wait" foraging strategy of *Coryphaenoides spp.* within a home range (Wilson and Waples, 1984) but early results showed these fishes to be highly mobile, exiting the detection range within 24 h (Priede and Bagley, 1991). Data analyses therefore focused on short-term, localized movements and feeding aggregation behaviours with sample sizes ranging from 1 to 63 individuals. These studies occurred in localized regions such as the Porcupine Seabight (n=5, 23%), Porcupine Abyssal Plains (n=5, 23%), and the North (n=6, 27%) and Central Pacific (n=2, 9%); consequently, there is low global coverage (**Table 3.1, Fig. 3.1**).

More recent acoustic telemetry studies involving the capture, tagging, and release of fish have covered regions from the Central and Eastern tropical Pacific, to the Azores and the Cumberland Sound in the Eastern Canadian Arctic, as well as the Indian Ocean's Great Australian Bight, to a maximum of 1200m depth. These studies have examined both vulnerable and protected species including two elasmobranchs (Bagley, 1993; Daley et al., 2015), and seven teleost fishes, including several commercially important species (Hussey et al., 2017; Weng, 2013). When reported, the non-detection rate of acoustic tags ranged between 0% and 52% of the total deployed tags per study (ranging from 1 to 223 tags deployed).

3.3.2.2 Satellite and archival telemetry study statistics

Satellite and archival telemetry have been used to record the movements of well over 1000 tagged individuals from 7 different families of deep-water fishes (**Tables 3.2 and 3.3**). These studies have been dominated by the Pleuronectids (n=17, 65% of satellite and archival studies), focusing on Pacific halibut (*Hippoglossus stenolepis*; Seitz et al., 2003, 2005, 2011; Loher and Seitz, 2006; Loher and Blood, 2009; Loher, 2011) (n=16, 62%), Greenland halibut (*Reinhardtius hippoglossoides*; Peklova, 2012; Boje et al., 2014) (n=2, 8%), and Atlantic halibut (*Hippoglossus hippoglossus*; Seitz et al., 2014; Armsworthy et al., 2014) (n=2, 8%). The remaining studies included 6 elasmobranch species (n=7, 27%; Hulbert et al., 2006; Peklova, 2012; Rodríguez-Cabello and Sánchez, 2014; Rodríguez-Cabello et al., 2016; Campana et al., 2015; Comfort and Weng, 2015; Shipley et al., 2017) and one additional deep-water teleost (n=1, 4%; Brown et al., 2013). Two studies which described the attachment of satellite tags to deep-water species (*Centrophorus spp.*, *Hexanchus griseus*, and *Hexanchus nakamurai*; Brooks et al., 2015, *Somniosus microcephalus*; Hussey et al., 2018) were not included in summary metrics due to a lack of reported tag depth records, however, their methodologies will be discussed later in this paper.

Study sites were primarily concentrated in Northern Pacific waters (n=16, 62%), particularly in the Gulf of Alaska and near the Aleutian Islands, however, satellite and archival studies were also conducted in both the North (n=9, 35%) and Southern Atlantic (n=1, 4%), as well as in Arctic deep-water regions (n=3, 12%) (**Fig. 3.1**).

Premature tag release was reported in 65% (n=15) of satellite studies and led to the exclusion of incomplete satellite archival datasets from certain analyses. Tag failures including failure to transmit to Argos, tag release complications (*i.e.*, software failure preventing release; Seitz et al., 2003), and lack of tag recovery for studies requiring archived data retrieval were reported in 61% (n=14) of satellite telemetry studies and resulted in significant loss of data. Reported tag failures affected up to 36% (n=14) of tags deployed by each study (5–138 total tags deployed per study). Fish recapture by commercial vessels prematurely terminated the monitoring of tagged individuals in three studies but provided access to valuable archival time series data stored on PAT tags (Seitz et al., 2003, 2011; Loher et al., 2008).

For archival studies, tag recapture rates varied from 6% (n=210; Boje et al., 2014, n=166; Loher, 2011) to 14% (n=14; Seitz et al., 2005) of total tags deployed per study. Overall, 94% (n=390) of all deployed archival tags were not recovered. Of these instances, only one tag loss was assumed to be due to tag failure (Boje et al., 2014). The remaining tag losses can be attributed to failure to recapture tagged animals.

3.3.3 Animal capture methods

Capture methods employed in deep-water telemetry studies depended largely upon the ability of target species to survive the extreme changes in ambient pressure and temperature experienced during transport between occupied depths and the surface (see further discussion of barotrauma and thermal stress in Section 3.4.6). As the resiliency of deep-water species to pressure-induced illness, or barotrauma (Carlson, 2012), is highly influenced by the presence of a swim-bladder (Colotelo et al., 2012), the capture methods examined were often reflective the target species' possession of this physiological trait or lack thereof.

3.3.3.1 Acoustic studies

Of the acoustic studies employing capture and release (36%, n=8), fish were caught using bottom longlines (Starr et al., 2000, 2002; Daley et al., 2015; Hussey at al., 2017; Barkley et al., 2018), bottom trawls (Barkley et al., 2018), commercial bottom angling gear (Weng, 2013), modified trolling gear (Starr et al., 2000, 2002), and by handlining (Afonso et al., 2012, 2014). Bottom longlines were set at depths between 400 and 1100m (Hussey et al., 2017) for durations of 3 (Daley et al., 2015) to 12 h (Hussey et al., 2017; Barkley et al., 2018). Bottom trawls for Greenland halibut were conducted at depths between 224 and 891m at a speed of 3 knots (~93 m/min; Barkley et al., 2018), while trolling speeds were maintained below 0.6 knots (20 m/min; Starr et al., 2000) to avoid decompression-related illness in captured rockfishes. For deep-water eteline snappers captured using commercial angling gear, excess gas was released from the swim bladders of swollen fish using a syringe before they were returned to depth using a weighted recompression device (Weng, 2013). Alternatively, rockfishes captured using a similar method were brought to a minimum depth of 20m (for underwater tagging, see Section 3.4.6) to avoid decompression issues (Starr et al., 2000, 2002). Seabream caught via handlining were targeted at depths <200m and were hauled to the surface at slow speeds (12 m/min; Afonso et al., 2012, 2014).

3.3.3.2 Satellite studies

Bottom longlines were the primary capture method for animals tagged in deep-water satellite telemetry studies (70%, n=16). In one study, Greenland sharks were tagged and monitored after being incidentally captured on commercial longlines targeting Greenland halibut (Campana et al., 2015). Main lines targeting study species generally exceeded 1000m length (Peklova, 2012; Rodríguez-Cabello and Sánchez, 2014; Rodríguez-Cabello et al., 2016) and were set at depths down to 1100m (Peklova, 2012). In most studies, bottom longlines were left to soak for between 6 and 12 h (Seitz et al., 2011; Peklova, 2012). The Spanish longlines used to target Patagonian toothfish extended beyond this depth (to a maximum of 1460 m) but were limited to less than 1800m depth to prevent tag release device (RD1800) activation when tagged fish returned to the bottom post-release (Brown et al., 2013). The shallowest recorded capture depths of between 500 and 750m were for Cuban dogfish (*Squalus cubensis*; Shipley et al., 2017), while the shortest soak times (2–3 h) were also used to target Cuban dogfish and the leafscale gulper shark (Rodríguez-Cabello and Sánchez, 2014; Rodríguez-Cabello et al., 2016; Shipley et al., 2017).

3.3.4 Tag attachment methods

The tag attachment methodology used in a given study typically depends on the physiology and life history of the target animal and is often adapted to allow tagging of diverse species or reduce the impact of tagging on animal behaviour.

3.3.4.1 Acoustic tag attachment

Acoustic tags were either attached externally (9%, n=2), surgically implanted in the peritoneal cavity (31%, n=7) or ingested by the target organisms (59%, n=13).

For external tag attachment, one study mounted VEMCO V16 tags to the first dorsal fin of adult southern dogfish (*Centrophorus zeehaani*) using two 4mm steel bolts with ‘Nyloc’ nuts and a backing plate (Daley et al., 2015). Two incidences of static depth data (over 100 sequential detections at a constant depth) were identified as post-release mortalities, as tag shedding was presumed unlikely given the strength of the attachment method (Daley et al., 2015). Another study used a manned submersible outfitted with a pneumatic gun to apply dart-mounted tags to the caudal fins of coelacanths *in situ* (Hissmann et al., 2000). Preliminary studies on the effects of this attachment method showed little evidence of altered swimming performance or behaviour and tags were retained for 3–4 weeks (Schauer et al., 1997).

Surgical implantation of tags, which is considered to extend tag retention and consequently the data collection period, was undertaken in seven studies on seven species: blackspot seabream (*Pagellus bogaraveo*), three species of deep-water eteline snappers (*Etelis coruscans*, *Etelis carbunculus*, *Pristipomoides filamentosus*), two deep-water rockfish (Greenspotted rockfish, *Sebastes chloristictus* and boccacio, *Sebastes paucispinis*) and one flatfish (Greenland halibut) (Afonso et al., 2012, 2014; Weng, 2013; Hussey et al., 2017; Barkley et al., 2018). Three studies used a similar methodological approach by placing fish into a tagging cradle and providing continuous gill irrigation during tagging procedures (Afonso et al., 2012, 2014; Weng, 2013). In two studies, tagging surgery was administered by divers using an underwater tagging bench suspended at a depth of 20m to reduce the likelihood of barotrauma (Greenspotted rockfish and bocaccio; Starr et al., 2000, 2002). In these studies, the additional precaution of a cage-release mechanism was used to return the tagged fish to the depth of capture, allowing time for post-tagging recovery and avoiding predation during descent (Starr et al., 2000, 2002). In all cases, researchers avoided the use of anaesthetic due to evidence suggesting it would result in prolonged recovery periods at the surface and/or high anaesthetic doses were required due to slow metabolism (Afonso et al., 2012, 2014; Weng, 2013; Hussey et al., 2017). Given the distance that tagged fish must travel to return to depth, coupled with the potential for increased predation risk during post-release recovery (see Section 3.4.6), the decision of whether to use anaesthetic must be considered in terms of the probability of survival for deep-water species.

The least invasive tagging approach, tag ingestion by fish (using baited transmitters deployed via AUDOS), was used to monitor individual movements from FFVs deployed to a maximum of 5900m depth (Priede et al., 1990a, 1990b, Priede and Bagley, 1991). This allowed observations of the movements of abyssal species, such as the grenadiers (*Coryphaenoides sp.*) which would not survive being brought to the surface due to extensive barotraumas and thermal stress (see Section 3.6). One of these studies produced the first movement data for two additional species, the Portuguese dogfish (*Centroscymnus coelolepis*) and blue hake (*Antimora rostrata*; Bagley et al., 1994).

3.3.4.2 Satellite tag attachment

Satellite tags were predominantly attached by darting (74%, n=17), via the implantation of an anchor (usually an umbrella tip or stainless-steel dart) into the musculature (typically dorsal) of the animal and connected to the tag with a strong leader (monofilament line or stainless steel). All studies on Pacific and Greenland halibut attached PSATs by darting. A titanium dart was inserted through the dorsal muscle (2.5–4 cm medial to dorsal fin) and pterygiophores on the ocular side of the flatfish to anchor the tag between the bony fin rays. This design was used to prevent muscle damage and tag rejection due to hydrodynamic drag. The dart was connected to a trailing PSAT by 15 cm of monofilament fishing line (130 kg test) wrapped in adhesive-lined shrink-wrap to increase the circumference and rigidity of the tether to prevent rubbing and decrease muscle and skin damage due to tag movement while swimming (Seitz et al., 2011; Loher and Clark, 2009). A similar approach was used for tagging Greenland sharks, where tag darts engaged the radials beneath the dorsal fin to reduce the chances of dislodgement, however, this study reported subtle modifications to leader strength (181 kg test) and sheathing (plastic tubing; Campana et al., 2015). For the flattened Arctic skate, tags were attached by a modified Peterson disc tagging procedure following previous work on a shallow-water skate (*Dipturus batis*, Wearmouth and Sims, 2009; Peklova, 2012). In this case, a steel wire was fed through the mid-section of a skate's wing and secured on either side (dorsal and ventral) by anchoring to a disc plate (Peklova, 2012). Due to a high rate of premature tag detachment reported by this study, it was suggested that a different tag attachment method should be considered for this species and for similar small-bodied batoids, such as the novel approach developed for attaching PSATs to short-tailed stingrays (Le Port et al., 2008). MiniPATs were mounted on leafscale gulper sharks using a unique attachment method whereby an anchor composed of a stainless-steel rod and holding the tag at its apex was attached at each end to a needle which penetrated the musculature at the base of the first dorsal fin (Rodríguez-Cabello and Sánchez, 2014). Finally, a recent study attached PSATs to the small-bodied Cuban dogfish using an approach aimed at minimizing invasiveness and increasing tag retention wherein a monofilament bridle was passed through the lower quarter of the anterior edge of the dorsal fin and secured under the trailing edge by a metal crimp (Shipley et al., 2017).

Informal telemetry guidelines suggest that a transmitter's weight should not exceed 2% of the body weight in air of the fish to be tagged (Brown et al., 1999). However, while this rule is widely accepted, it may not be universally applicable. Some studies suggest that tag type and attachment method may have a larger impact on impeding normal swimming behaviour than tag weight; for example, the long antenna of a satellite tag may interfere with a fish's tail while swimming (Brown et al., 1999; Seitz et al., 2003). To determine the smallest size of halibut that could be equipped with satellite tags, observations of an 86 cm fork length (FL) fish tagged under experimental conditions (Loher, 2006, unpublished data), were conducted by one of the reviewed studies. By modifying leader length and tag orientation it was possible to minimize tag effects on the swimming behaviour of smaller fish and consequently the acceptable length of PAT-tagged Pacific halibut was reduced from 105 to 82 cm (Loher and Clark, 2009). This method was readily adopted by later studies (Seitz et al., 2011; Peklova, 2012). Despite these efforts, it is important to note that the size range of fishes decreases with increasing depth until an optimum size of <30 cm LT is reached at extreme depths (Priede, 2017). This implies that at extreme depths (and particularly hadal depths, >6000 m), few species are big enough to be considered for tagging (I.G. Priede pers. comm.).

3.3.4.3 Archival tag attachment

For one study which deployed LTD1300 long-term archival tags on Pacific halibut, tags were mounted on PVC cradles padded with silicon sheeting (4.8 mm, 30 durometer hardness) and secured near the dorsal fin on the ocular side using an 18 AWG monel wire attached to a padded backing plate on the non-ocular side (Loher, 2011). Intra-coelomic surgical implantation was used for Mk9 archival tags also deployed in this study, resulting in a 19.5 cm stalk left protruding perpendicularly from the dorsal surface of the animal (Loher, 2011). These attachment methods were chosen after a multi-year study demonstrated their ability to improve tag retention and reduce the minimum size of tagged Pacific halibut as compared to the attachment of satellite tags via darting (Loher and Geernaert, 2011). A long-term holding study comparing internal archival tag implantation approaches also described the latter procedure for Mk9 implantation and reported no evidence of negative effects on fish growth or behaviour after 1 y post-surgery (Loher and Rensmeyer, 2011).

3.3.5 Study purpose

3.3.5.1 Acoustic telemetry to assess the foraging behaviours of abyssal fishes

Early tracking data for tagged grenadiers demonstrated an active foraging search strategy that favoured cross-current movement trajectories (Bagley, 1993) and led to the rapid lateral dispersal of nutrients at the sea floor (Priede et al., 1990a, 1990b, 1994; Priede and Bagley, 1991; Armstrong et al., 1991). These studies also showed that seasonal and regional variation in surface productivity significantly affected grenadier density and behaviour (Priede and Bagley, 1991; Armstrong et al., 1991), resulting in more rapid swim speeds, arrival rates, and departures from bait stations following peak periods of nutrient export from the photic zone (October versus February; Bagley, 1993; Bagley et al., 1994; Armstrong et al., 1992; Priede et al., 1994). Preliminary records showing a strong association of grenadiers with the benthos (Priede and Smith, 1986; Priede et al., 1990a, 1990b) were contrasted by later observations suggesting that vertical excursions (> 15m above the substrate) might enhance foraging ability in oligotrophic regions by increasing the likelihood of encountering odour plumes (Armstrong et al., 1991). Regional abundance calculations using the time of first arrival (Wilson and Smith, 1984; Priede and Smith, 1986), since adapted to examine the abundance of another prominent deep-water species (the Greenland shark, *Somniosus microcephalus*; Devine et al., 2018), demonstrated lower grenadier densities in nutrient poor regions of the N Pacific and N Atlantic (Priede et al., 1990a, 1990b; Armstrong et al., 1992). Prolonged lingering of fish near bait stations also observed in these regions (Priede et al., 1990a, 1990b; Armstrong et al., 1992) led to large localized congregations near bait sources despite low regional abundances (Priede et al., 1990a, 1990b; Priede and Bagley, 1991; Armstrong et al., 1992).

Over the following decade, technological advances including the implementation of more sophisticated transponders (CATs) and scanning directional sonar systems (Bagley, 1993) allowed the simultaneous tracking and identification of multiple tagged individuals and refined methods to accurately measure localized grenadier movements (Bagley, 1993, Bagley et al., 1994; Collins et al., 1998; Fig. 3). Studies employing these advanced technologies recorded findings that contradicted many of the foundational observations on grenadier movements and nutrient dispersal in the deep sea (Smith et al., 1997; Collins et al., 1998). For example, one such study reported no seasonal differences in the response time or departure rate of abyssal grenadiers to and from a simulated food-fall (baited FFV) and significantly reduced rates of nutrient dispersal relative to previous observations from the same region (Smith et al., 1997). Despite relatively rapid swim speeds, the movement trajectories of tagged grenadiers were highly convoluted, leading to radial fish dispersal rates which were three times lower than expected (Smith et al., 1997). Additionally, the observed departure of individuals from bait stations before peak numbers were attained led researchers to suggest that previous photographic estimates of population size may have been underestimated (Smith et al., 1997). An apparent shift in the population size structure of grenadiers in the abyssal NE Atlantic to smaller individuals was also observed, however, this may have been an artifact of the seasonal migration of mature animals away from the study site (Smith et al., 1997). Previous estimates of the rate of radial food fall dispersal were revised from 6.96 m/min to a mere 1.05 m/min, a discrepancy which was attributed to error derived from the use of pinger signal attenuation to estimate range in earlier studies (Collins et al., 1998).

The era of abyssal tracking studies ceased in 1999 following a final investigation where a further demersal species, the blue hake (*Antimora rostrata*) was tracked in conjunction with abyssal grenadier (Collins et al., 1999). While not the only study to report tag ingestion by a non-macrourid species (*e.g.,* the Portuguese dogfish, *Centroscymnus coelolepis* and *A. rostrata*; Bagley, 1993; Bagley et al., 1994), this study used three measures of activity; arrival at bait, tail-beat frequency, and departure swimming speeds, to provide a novel comparison of the movement behaviours of these two deep-water species. The authors reported contrastingly high activity levels for blue hake and suggested that while an extremely slow metabolic rate may allow abyssal grenadiers (*C.(N.) armatus*) to dominate at depths beyond 2500 m, the faster metabolism and response rate of the blue hake, fueled by higher nutrient availability, might allow grenadiers to be outcompeted at shallower depths (Collins et al., 1999).

3.3.5.2 Acoustic telemetry as a tool for effective deep-sea species management

Much like remote tagging of abyssal fishes, novel approaches in the capture, handling, and release of tagged fish (see Section 3.4.6) have allowed researchers to answer important questions regarding the spatial ecology and management of several deep-sea species. One study recorded the movements of three deep-water eteline snappers (*Etelis coruscans*, *Etelis carbunculus*, and *Pristipomoides filamentosus*) within a fishery closure area to examine the efficacy of marine reserves as a tool for fisheries management (Weng et al., 2013). Detection data for the deep-water longtail red snapper (*E. coruscans*) and deep-water red snapper (*E. carbunculus*) suggested that while both species are likely afforded some protection by the fishery closure, a higher frequency of movement by the former (*E. coruscans*; including movements across the closure boundary) likely decreases the effectiveness of the marine reserve for this species (Weng et al., 2013). In contrast, low rates of horizontal movement and a high degree of residency reported for the southern dogfish (*C. zeehaani*) suggested that the depth range and along-slope extent of a fishery closure were sufficient to encompass a high proportion of the local population (Daley et al., 2015). For species that are highly sensitive to the effects of barotrauma, such as deep-water rockfishes (e.g., *S. chloristictus* and *S. paucispinis*), specialized protocols were used to reduce tagging stress and increase survival rates in order to monitor the movements of target animals at depth (see Section 3.4.5) and evaluate the effectiveness of area management strategies (Star et al., 2000, 2002).

In addition to the assessment of existing management tools, acoustic telemetry data has contributed to the movement of a fisheries management boundary in the case of one deep-water Arctic flatfish (the Greenland halibut, *R. hippoglossoides*; Hussey et al., 2017). By combining data on the movements of tagged fish (displaying extensive horizontal mobility and inshore and offshore residency) as well as fisheries and environmental records, researchers were able to directly impact management decisions to improve the sustainability of an important Inuit fishery (Hussey et al., 2017; **Fig. 3.3**). The continued monitoring of Greenland halibut in polar waters has further demonstrated the complexity of managing highly mobile commercial species and highlighted the importance of considering inshore-offshore connectivity to ensure sustainable fisheries management (Barkley et al., 2018).

The importance of spatial ecology for fisheries management was also identified for a commercial species inhabiting the slopes of deep-water seamounts (Afonso et al., 2012). Two studies examining the movements of blackspot seabream showed a high degree of variability in individual movement patterns but were nonetheless able to define distinct patterns in residency and vertical movement behaviour (Afonso et al., 2012, 2014). The first study identified two patterns in site attachment, where some fish appeared to remain highly resident to a discrete region of the seamount over long periods (6 mo. to 2 y), while others were only detected for a few weeks before migrating away from the study site (Afonso et al., 2012). In addition, increased nocturnal detection rates suggested that tagged fish were undertaking either horizontal, or more likely vertical, diel migrations (Afonso et al., 2012). Expanding on this work, researchers adapted their protocols to improve fish survival rates (see Section 3.4.5) and incorporated the use of pressure-sensitive acoustic tags and mobile acoustic telemetry to further examine the potential for vertical diel movement patterns (Afonso et al., 2014; **Fig. 3.3**). This study was the first to document the fine-scale three dimensional movements of a deep-water species and successfully detected extensive vertical migrations occurring at both short-term (tidal/diel) and long-term (seasonal) temporal scales (Afonso et al., 2014). Moreover, these movement patterns suggested a seasonal switch in the diel behaviour mode of the seabream (shallower benthic behaviour in winter months vs. deeper, more pelagic behaviour in summer/autumn) potentially reflecting adaptation to differences in prey availability (Afonso et al., 2014).

3.3.5.3 Examining seasonal movement behaviours in demersal teleost fishes via satellite telemetry

In the case of two deep-water flatfishes (Pacific and Greenland halibut), course-scale movement trajectories and temperature and depth-related behaviours recorded by satellite and archival telemetry clarified the timing and locations of biologically important behaviours with implications for fisheries management. A number of these studies examined the timing and direction of winter spawning migrations and population substructure of Alaskan and Canadian Pacific halibut (Seitz et al., 2017; **Table 3.2**), addressing questions which were of critical importance for fisheries management given pressure from NW Pacific fisheries organizations to extend the fishing season into the winter closure period. The earliest of these studies marked the first use of popoff archival transmitting tags (PAT) to examine the movement behavior of a deep-water demersal species, recording fine-scale vertical behaviours which could not be assessed through traditional sampling methodologies (*e.g.,* stock assessments using benthic fishing gear; Seitz et al., 2003). The application of PATs also ensured a high rate of fisheries-independent tag returns and the collection of valuable data for fish that travel large distances or to unexpected locations (Seitz et al., 2003). Continued satellite telemetry studies highlighted the characteristics of fall spawning migrations (northward and offshore movements in the Gulf of Alaska; Loher and Seitz, 2006), indicating variable movement behaviours among individuals and refuting the assumption that Pacific halibut spawn annually (Loher and Seitz, 2008; Seitz et al., 2005). While some evidence of cross-boundary movements was also recorded (Loher and Clark, 2009), Pacific halibut showed a high degree of site fidelity and active homing to summer feeding grounds, supporting the occurrence of locally resident Pacific halibut subpopulations in the

Aleutian Islands region and Bering Sea (Seitz et al., 2007, 2008, 2016; Loher et al., 2008). Importantly, these telemetry data showed a distinct mismatch in seasonal fisheries closures in relation to the spawning periods of Pacific halibut. This suggests that the seasonal opening of the commercial fishery in Gulf of Alaska has historically preceded the termination of spawning by weeks or months, in turn, leading to the interception and capture of halibut returning to summer foraging grounds (Loher and Blood, 2009; Loher, 2011).

In the Eastern Canadian Arctic, time series depth/temperature data from satellite tags showed Greenland halibut to have a preference for deep (>900 m), cold (~2.3 °C) waters, however, seasonal movements between deeper, warmer waters in the fall months and shallower, colder regions in the winter and spring were observed, corresponding to the presence/absence of sea ice (Peklova, 2012). The strong site fidelity for deeper regions from August to November was also correlated with the location and timing of a trial summer commercial Greenland halibut fishery, while time spent in shallower colder regions was likely associated with the winter fishing ground in the northern section of the Sound (Peklova, 2012). These data provided the first evidence for the seasonal migration of fish within Cumberland Sound that were later shown in detail using acoustic telemetry (Hussey et al., 2017). Similarly, in western Greenland, archival-tagged Greenland halibut followed predictable seasonal migrations between deep waters and shallower, ice-covered fjords, and recorded the first seawater temperature measurements taken beneath the Jakobshavn Isbræ outlet glacier (Boje et al., 2014).

In the Southern Atlantic, satellite tag data for an additional commercial species, the Patagonian toothfish, revealed strong site fidelity over a 6-month period, while archived depth records were used to infer three behavioural patterns, including both foraging and spawning, as well as seasonal depth preferences (Brown et al., 2013). Repeated movements to shallower waters (900–1200 m) were associated with the summer spawning period, while movements to deeper water during the post-spawning months were thought to allow fish to take advantage of more readily available prey (Brown et al., 2013).

3.3.5.4 Advancing knowledge of the vertical and horizontal movements of deep-water chondrichthyans

Despite concerns over their vulnerability to exploitation, many deep-water chondrichthyans remain data deficient, with a significant lack of knowledge regarding population connectivity and scales of movement. The first study to deploy PATs on a deep-water shark, the leafscale gulper shark, found that animals captured at depth (900–1100 m) could be successfully brought to the surface, tagged and released (Rodríguez-Cabello and Sánchez, 2014). The authors reported large horizontal displacements of tagged animals (up to 287 nm), supporting the suggestion of a single population in the NE Atlantic with implications for stock management (Rodríguez-Cabello and Sánchez, 2014). A later study on the same species built on these previous findings by combining tag data and ARGOS float profiles to further elucidate the movement pathways of tagged sharks (Rodríguez-Cabello et al., 2016). This study showed variability in both horizontal and vertical movements among individual sharks, however, tag release locations suggested that preferred pathways may be used (Rodríguez-Cabello et al., 2016). Additionally, this study provided further support for large-scale horizontal movements of this species and illustrated their ability to undertake large vertical excursions above the abyssal plain (Rodríguez-Cabello et al., 2016).

For a second data deficient deep-water shark (the Cuban dogfish), high resolution time-series temperature and depth data demonstrated that tagged sharks were subjected to high rates of predation during daylight hours (Shipley et al., 2017). This study also proved the effectiveness of a novel cage-release mechanism at preventing predation and facilitating recovery following tagging (Shipley et al., 2017). Vertical habitat data suggested that the sharks undertook diel vertical migrations and inhabited a broad range of depths and temperatures which may be related to a preference for specific bathymetric structures (Shipley et al., 2017). Similarly, distinct diel patterns in vertical movement were recorded for the much larger bodied bluntnose sixgill shark (*H. griseus*), where vertical speed was found to correlate with photic zone light levels and was indicative of more active foraging occurring nocturnally in shallow waters (Comfort and Weng, 2015; Fig. 3).

Satellite and archival data for two Arctic chondrichthyans, the Greenland shark and Arctic skate (*Amblyraja hyperborea*), showed that both species occupied broad depth ranges (0–1816m and 500–1300, respectively; Table 2), while Greenland sharks also encountered a wide range of temperatures (0–17.2 °C, Campana et al., 2015; Peklova, 2012). Although the tag release locations of Arctic skate demonstrated relatively limited horizontal displacements, vertical movement data suggested that skates exhibited a range of activity levels, ranging from periods of no movement to high activity, and including movement rates that exceeded those of other flat-bodied fishes (Peklova, 2012). Conversely, tagged Greenland sharks were shown to undertake vast horizontal movements, suggesting the need for regional trans-boundary management of the species as there is likely little impediment to genetic mixing across ocean basins (Campana et al., 2015).

3.3.6 Challenges of tagging deep-water species

In recent decades, tagging methodologies have seen vast improvements to increase the rate of survival of deep-water animals that are captured at depth and released at the surface, including the use of recompression devices (Weng, 2013), underwater tagging (Starr et al., 2000, 2002), and *in situ* tagging using submersibles or ingestible tags (Hissmann et al., 2000; Priede et al., 1986, respectively). Despite these efforts, mortalities resulting from tagging procedures pose a major impediment to the effective and ethical study of deep-water species. For most fish, the biggest physical challenge occurs during the animal's trip to the surface, as changes in pressure are often extreme and occur rapidly. This is critical for physoclistous teleosts, as pressure changes in the swim-bladder are controlled by the diffusion of gases into and out of the vascular system, a process requiring time for acclimatization and gradual movement across a pressure gradient. The abrupt changes in pressure that occur during the retrieval of a captured fish from depth often exceed the volume adjusting capacity of the swim-bladder, occasionally leading to its expansion and rupture (Sigurdsson et al., 2006). This can in turn cause the eversion of the esophagus through the mouth, resulting in the bruising, hemorrhaging, and displacement of the internal organs (Hannah et al., 2008). Recompression techniques involving the release of fish at the depth of capture (where gas volume is returned to pre-capture levels) have shown promise for improving the short-term survival rates of physoclistous teleosts suffering from barotrauma when compared to those released at the surface (*e.g.*, yelloweye rockfish, *Sebastes ruberrimus*; Hochhalter and Reed, 2011). However, other gas-related injuries such as exopthalmia (bulging of one or both eyes), and emphysema (abnormal inclusion of gas into various tissues), caused by the escape of excess gas, can lead to other serious injuries such as optic nerve damage, which can impede an animal's ability to engage in normal behaviours (Rogers et al., 2008; Hannah et al., 2008). Long-term consequences of decompression, including the loss of visual orientation and an inability to maintain neutral buoyancy, have been observed for several weeks following the capture and recompression of rockfish, and are thought to limit the animal's natural behaviours and ability to avoid predation (Rankin et al., 2017). Further study of these factors on the long-term survival of tagged fish is thereby warranted, given the longevity of this, and many other deep-water species.

Capture methodologies used to tag deep-water fish have included preventative measures to mitigate at vessel mortality associated with barotrauma and minimize the stress of tagging individuals at the surface. For example, in studies involving black-spotted seabream, barotrauma was avoided by targeting fish at <200m depth, minimizing the absolute rate of change in pressure during transfer to the surface (Afonso et al., 2012, 2014). The natural release of excess gas from the swim-bladder during depressurization was also achieved by maintaining a slow rate of retrieval (0.2 m/sec), thereby reducing the risk of swim-bladder rupture. In cases where fish still showed signs of over-inflation after being brought to the surface, excess gas was removed via the insertion of a hypodermic needle into the swim-bladder (Afonso et al., 2012; Weng, 2013) and everted stomachs were pushed back in through the mouth using a smooth rod following venting (Weng, 2013).

In addition to pressure-related injuries, thermal stress can equally impact the health of deep-water animals tagged at the surface. This is especially important in equatorial regions where marked thermoclines exist and where at-vessel mortality has been shown to increase with depth of capture (Brooks et al., 2015). For example, Cuban dogfish released following tagging at surface temperatures of 30 °C during the day, exhibited very little movement (Talwar, 2016) compared to those which were captured and released under much cooler temperature conditions (15–25 °C) (Daley et al., 2015). These data showed that post-release behaviour and recovery of southern dogfish was highly correlated with surface temperature upon release (Brooks et al., 2015; Daley et al., 2015; Talwar, 2016). In the latter study by Daley et al. (2015), the temperature differential between the surface and depth was purposefully reduced by only fishing during cool winter nights to minimize capture stress.

Fishing gear type and soak time can also affect the survivability of captured deep-water fish (Simonsen and Treble, 2003; Dapp et al., 2016). However, the type of fishing method depends on the target species and must be assessed based on its lifestyle and physiology, particularly its mode of respiration (Dapp et al., 2016). For example, restricted mobility due to longline or gillnet capture can cause fish to undergo exhaustive anaerobic exercise leading to respiratory hypoxia in species that rely heavily on ram ventilation (Dapp et al., 2016; Mandelman and Skomal, 2009). Stress incurred while fighting on the line can also have serious detrimental physiological effects which may be lethal in some species (Manire et al., 2001; Mandelman and Skomal, 2009). Plasma lactate levels have been shown to be positively correlated with the level of exertion exhibited while struggling on the hook in some pelagic sharks (Gallagher et al., 2017), the extent of which is thought to also lead to respiratory and metabolic acidosis and thereby an increased susceptibility to mortality (Manire et al., 2001; Mandelman and Skomal, 2009). The susceptibility of sharks to the physical stresses associated with longline capture appears to differ according to species as well as set duration (Mandelman and Skomal, 2009; Barkley et al., 2017). While the motivation used to designate fishing set duration were not explicitly stated in the reviewed telemetry studies, those targeting deep-water sharks reported the shortest set durations overall (2–3 h) (Rodríguez-Cabello and Sánchez, 2014; Rodríguez-Cabello et al., 2016; Shipley et al., 2017).

For some species, descent to their preferred depth following tagging can be equally as hazardous as the initial ascent, as capture-based effects such as the loss of equilibrium can increase an individual's risk of predation (Rankin et al., 2017; Shipley et al., 2017). For species such as the gulper sharks (*Centrophorus spp.*), the risk of predation is thought to be particularly high (Brooks et al., 2015); a problem which can lead to lost data and reduced sample sizes. In a study examining Cuban dogfish, this risk was mitigated by using free-divers to manually release animals between 10 and 20m depth, or by employing a mechanised cage with a rotating door to protect individuals from predation during descent (Shipley et al., 2017). Similar cage mechanisms have been employed for the study of shallow-water species, such as the grey triggerfish (*Balistes capricus*; Williams et al., 2015), as well as deep-water teleosts like the Greenland halibut (Simonsen and Treble, 2003) and deep-water rockfishes (Greenspotted rockfish and bocaccio; Starr et al., 2000, 2002), providing additional support for the success of the latter technique.

Attempts to overcome the hurdles associated with the ascent and subsequent descent of deep-water species tagged at the surface have shifted the focus of many researchers to the development of *in situ* tagging methods, leading to creative solutions such as an under-water tagging bench used by divers to tag captured specimens at greater depths (Starr et al., 2000, 2002; Hislop, 1969). Underwater tagging equipment (UTE) such as autonomous tagging devices (Sigurdsson et al., 2006; **Fig. 3.4**), and manned submersibles used to shoot darts containing acoustic transmitters (Schauer et al., 1997; Hissmann et al., 2000; **Fig. 3.4)** have also been employed to remotely tag deep-living teleosts *in situ*. Additionally, baited acoustic transmitters deployed from FFVs have provided an effective means of tracking specimens at extreme depths while eliminating the stresses of conventional tagging procedures (Priede and Smith, 1986; Armstrong et al., 1991, 1992; **Fig. 3.4**). Due to their relatively low metabolic rates, it has been suggested that ingested transmitters could be retained for longer periods of time by deep-sea fishes relative to their shallow-living counterparts, thereby increasing potential tracking durations (Bagley et al., 1999). These studies are, however, limited by the willingness and ability of target species to ingest the tags, and have therefore been largely restricted to monitoring the movements of grenadiers (genus *Coryphanoides*) (**Table 3.1, Figs. 3.3 and 3.4**). Given the extreme longevity and low fecundity of many deep-water species (see Introduction), it is critical that capture-induced stress and post-release mortality associated with tagging (whether at depth or surface) are assessed and minimized to ensure studies meet appropriate animal welfare standards and to limit negative impacts on the population.

3.3.7 Future directions

3.3.7.1 Deep-sea fisheries and the fate of the deep ocean

To date, much remains to be discovered about the diversity, structure, and function of deep-sea ecosystems. However, despite its remoteness and inaccessibility, advances in deep-sea research have shown that much life in the deep sea is dependent on nutrients transported from terrestrial sources and the photic zone (Smith et al., 1997), and that these ecosystems are intrinsically linked through the exchange of matter and energy (Armstrong et al., 2012) and biogeochemical cycling (Dell'Anno and Danovaro, 2005). Pioneering deep-sea exploration has also shown the deep sea to be less pristine than previously imagined (Armstrong et al., 2012; Ramirez-Llodra et al., 2011). This evidence documents decades of hazardous waste disposal, natural resource extraction (Benn et al., 2010), and fisheries exploitation (Norse et al., 2012). With global shifts transforming the human relationship with the deep sea from one defined by waste disposal to one of exploitation (Ramirez-Llodra et al., 2011), in addition to climate-induced fluctuations in ocean temperature and acidity, deep-ocean ecosystems are now facing an immediate threat of intense disruption.

Baseline research on deep-sea ecosystem function, biological hotspots, and species dispersal will be essential for enabling environmental impact assessments to monitor the impacts of these recent human developments. Intergovernmental organizations such as the United Nations Regional Seas conventions have initiated the development of marine environmental policies and established a need for monitoring and reporting in the deep-sea (Benn et al., 2010). The ideals of fisheries and conservation management have also been combined through a coalition of the North East Atlantic

Fisheries Commission (NEAFC) and the OSPAR Commission established in 2008 to create rules concerning the sustainable governance of new and existing high seas fisheries (OSPAR, 2008; Benn et al., 2010). If focus is placed on matching the rate of advancement of deep-water telemetry with that of deep-sea exploitation technologies, biotelemetry will become an invaluable tool in meeting these demands in coming years.

3.3.7.2 Deep-sea fisheries

Following declines in catch rates for commercial shallow-water species, the rapid expansion of commercial deep-water fisheries over the past six decades has led to an industry that contributes between 800,000 and 1,000,000 t of marine fish to the global market annually (Koslow et al., 2000) while simultaneously encroaching on the last refuges of many pelagic species and leading to the overexploitation of inherently susceptible deep-water species (Norse et al., 2012). *K*-selected life history strategies common amongst deep-water fishes indicate unreliable recruitment success leading to high vulnerability to fisheries exploitation (Jennings et al., 1998; Roberts, 2002). Famous examples of mismanaged deep-water fisheries in Ireland, New Zealand, and Atlantic Canada (orange roughy, *H. atlanticus*, and Northern cod, *Gadus morhua*) have demonstrated the potential for previously unexploited stocks to become rapidly decimated to the point of commercial extinction (in ~10 yrs; Roberts, 2002, Clark et al., 2000, Norse et al., 2012) and continue to show few signs of recovery despite longstanding moratoria (Haedrich et al., 2001).

Currently, the rate of fisheries expansion far exceeds the advancement of technology available to monitor the movements of deep-sea species (Devine et al., 2006; Haedrich et al., 2001). While commercial fisheries have the financial means and incentives to drive technological advancements in monitoring, the challenges highlighted in this review have largely limited the potential appeal of research. To date, telemetry studies have attempted to overcome these challenges by pushing the limits of available technologies (Hussey et al., 2017), or through personal inventions (Priede and Bagley, 2000) (see Section 3.4.7.3), but these efforts are currently not sufficient to provide the monitoring that will be required in the deep-sea in the near future. Telemetry in the photic zone is a proven tool for collecting data to improve the accuracy of stock assessments, define management boundaries, and establish and assess the efficacy of marine protected areas (Crossin et al., 2017; Hussey et al., 2017). Biotelemetry approaches can also answer key questions on the behaviours underlying stock structure, such as migration routes and home ranges (Crossin et al., 2017; Hussey et al., 2017), explain variation in movements across population subsets and life history stages (Péron and Grémillet, 2013), and direct management policies to minimize effort and the scale of areas in need of protection while maximizing the benefit for species sustainability (McClellan et al., 2009; Maxwell et al., 2011). Static acoustic telemetry using receivers deployed beyond their maximum depth rating has thus far been the only way to observe the movements of deep-living species (*R. hippoglossoides*) over long timescales (≤2 y; Hussey et al., 2017). As longevity plays a key role in the inherent vulnerability of deep-water species (Devine et al., 2006), behavioural monitoring at appropriate timescales should certainly be considered for species susceptible to overexploitation and should be accurately incorporated into commercial targeted fishery and bycatch quotas. The oceanographic data obtained from sensors deployed on static telemetry moorings are also crucial for understanding the drivers of animal movements and for documenting environmental conditions in the deep-sea (Hussey et al., 2017). The following sections highlight possible approaches to advance deep-sea biotelemetry to assist the management, monitoring, and conservation of deep-water species.

3.3.7.3 Improving equipment design

The first studies to monitor deep-water species were reliant on custom built equipment (Priede and Smith, 1986; Bagley and Priede, 1997; Priede and Bagley, 2000). These studies showed rapid technological advancement early on, but development ceased in the late 90s and has not been reinitiated. This indicates that the resources and effort required to design systems to monitor the movements of deep-water species, while crucial to the establishment of deep-sea telemetry, have yet to be translated into practical tools that are accessible to a wide range of researchers. High production costs and a perceived limited market have likely reduced the appeal of telemetry manufacturers to develop and produce such equipment. In contrast, the availability and mass manufacturing of standard telemetry equipment (*e.g.,* VEMCO) has broadened the range of habitats and species studies, and number of users employing telemetry on a global scale (Hussey et al., 2015). This, in turn, has facilitated the growth of large-scale telemetry networks that allow interinstitutional cooperation and data sharing, promoting continued growth (Hussey et al., 2015). However, the ease of using this readily available commercial infrastructure and its application by the vast majority of users may be responsible for stunting the development of new forms of telemetry technology and analyses. The innovative engineering of new equipment and experimental design, like those developed in the infancy of biotelemetry, will be essential for the progression of monitoring species movement behaviours in the deep sea. Importantly, to promote the development of a commercial industry and the widespread availability of deep-water telemetry technologies, innovations in equipment design must also strive to limit development and production costs to the greatest extent possible.

Currently, equipment design (and therefore maximum depth ratings) restricts the use of most types of available telemetry equipment for deep-water monitoring. However, minor modifications to existing telemetry equipment could ease these constraints. For example, the depth ratings of satellite tags could be increased to withstand greater pressures by modifying the housing thickness or by replacing the existing material with one that is less easily compressed, such as titanium. Float material and design would also have to be improved with increases in maximum release depth, as the force of buoyancy exerted by the float must exceed that of the water pressure at extreme depths. These modifications would likely result in increased tag size, potentially restricting their use to large-bodied animals, but material advances may help to overcome this problem. Similarly, acoustic receivers could be modified to withstand greater depths by constructing housings using a more durable material, as well as by removing the air from any internal cavities and replacing it with an acoustically conductive fluid such as castor oil (Priede and Bagley, 2000). This would prevent the collapse of gear under pressure and eliminate the risk of gas expansion upon retrieval to the surface. While hydrophones have alternatively been used to detect acoustic tag transmissions at abyssal depths (up to ~5800 m) over short durations (< 24 h; Priede and Smith, 1986; Armstrong et al., 1991), the long-term effects of extreme pressures on this equipment are not well known. Testing to determine whether these hydrophones will remain functional over extended time periods in deep water must therefore precede their application in long-term acoustic telemetry studies in the deep sea.

The oceanographic data collected by animal-borne satellite archival tags have already vastly improved our understanding of global oceanographic processes and allowed data collection to occur in otherwise inaccessible regions (Lydersen et al., 2002; Roquet et al., 2013). By improving the depth ratings of these instruments and expanding their scope to deployments in the deep ocean, we could start to record largescale deep-sea oceanographic processes which would otherwise be impossible or too costly to observe. Deep-sea species, similar to marine mammal oceanographers (Lydersen et al., 2002) provide an economical platform for deriving big data for the deep sea.

3.3.7.4 Adapting existing technologies for use in the deep sea

Currently, VEMCO Mobile Transceivers (VMTs) are rated to depth of 1000m (double that of VR2 and VR receivers; available in plastic and titanium housings) and are mounted on large animals to transmit and detect the signals of other acoustic transmitters when in range (Holland et al., 2009; Lidgard et al., 2012; Broell et al., in review). These miniaturized receivers were primarily designed for examining intra- or interspecies interactions (Holland et al., 2009), however, they can also be attached to fixed moorings in place of traditional receivers and used to monitor species tagged at greater depths. Further field testing will nevertheless be required to determine their relative detection efficiency and detection radius at depth following initial work by Lidgard et al. (2012). Furthermore, VMTs could be attached to large, mobile deep-water species to monitor the movements of tagged fish outside the range of fixed arrays. However, due to the need for the physical retrieval of VMTs to obtain archived detection data, modifications allowing remote data transmission or tag retrieval are required. For example, by incorporating Bluetooth capabilities, VMTs can be linked with PATs, allowing data to be transmitted via satellite (similar to previous work by Lidgard et al., 2014). Alternatively, VMTs can be integrated into recoverable float packages that pop off at known locations that are easily accessible for retrieval.

The absence of light in deep-water regions poses further constraints as it impedes the use of light sensors on satellite tags to resolve geolocation estimates from the timing of sunrise and sunset. Researchers have bypassed this restriction by retrospectively calculating geolocation estimates for fish outfitted with archival tags by matching models of other environmental variables in the study region to data collected by sensors on the tags. For example, the movements of Atlantic cod in Massachusetts Bay and the North Sea were determined by comparing the pressure recordings on archival tags at specific dates and times to data predicted by a regional tidal model (Gröger et al., 2007; Pedersen et al., 2008). This approach, first developed for tracking plaice (*Pleuronectes platessa*; Metcalfe and Arnold, 1997), has paved the way for studies incorporating other environmental data archived by electronic tags (*e.g.,* temperature, salinity, ambient pressure, tidal patterns and bottom depths) to more accurately extrapolate geolocation estimates from complex oceanographic models for other marine species (Neuenfeldt et al., 2007; Skomal et al., 2009). While these studies set a benchmark for progress in deep-water tracking, little evidence has been presented to validate estimated locations using these models. A combination of multiple mark-report satellite tags (mrPAT) and an additional pop-off archival satellite tag deployed on a large deep-water predator provided the first example of a semi-continuous horizontal movement track for a deep-water species, as well as an approach for validating location estimates retrospectively calculated using environmental data (Hussey et al., 2018). mrPATs were programmed to pop-off every 8–10 days, producing a sequence of location estimates corresponding to the shark's trajectory, while a miniPAT was programmed to record temperature and depth data every 75 s for the entire tracking duration. By comparing mrPAT location data with the satellite geolocation estimates produced by miniPAT depth-temperature time series data coupled with oceanographic data, the accuracy of the above retroactive modelling approaches could be evaluated (Hussey et al., 2018).

Existing telemetry equipment could be used for applications beyond their intended purpose without requiring extensive design modifications. Tag lifespans (limited by battery life and memory) currently restrict the longevity of telemetry studies but may be particularly important for observing the movements of long-lived, deep-water species over extended time periods. Long-lifespan acoustic tags (~10 years) and extensive off-the-shelf acoustic telemetry infrastructure have allowed the monitoring of deep-water animal movements to occur over large spatiotemporal scales (Hussey et al., 2017; Barkley et al., 2018). The use of battery-less piezoelectric acoustic tags which harness power from the swimming motion of the host fish (Li et al., 2016), or hydrodynamically-charged external tags with built-in propellers, could extend the longevity of acoustic studies almost indefinitely, particularly given lower rates of biofouling in the deep-sea. However, since metabolic rates of deep-sea fishes are much lower than for shallow-water species the amount of energy available to be harvested for a transmitter would be reduced correspondingly (Priede, 2017).

Autonomous underwater vehicles (AUVs) can be outfitted with a variety of environmental sensors, directional hydrophones and acoustic receivers, and can self-navigate across vast ocean regions, recording oceanographic data and acoustic tag detections. Energy gathered through movement using changes in buoyancy (Slocum glider, Teledyne Marine, 2017 Dec 13), or a combination of solar and wave energy (Wave glider) supplements internal batteries allowing deployments of up to 1 year (Wave glider; Liquid Robotics, Energy Harvesting Ocean Robot, 2017 Dec 13). The Ocean Tracking Network (OTN, Dalhousie University, NS), a global acoustic telemetry network, currently uses gliders to monitor oceanographic conditions, download archived detection data from fixed receivers (Halifax Line, OTN, 2017 Dec 13), and collect independent detection records of tagged fish via onboard receivers (OTN, 2017 Dec 13). Given the logistical constraints and high cost of deploying and retrieving deep-water acoustic receivers, gliders could be used to remotely download detection records from fixed receivers. Gliders also provide a clear alternative to independently monitor tagged animals through programmed systematic surveys.

Additionally, AUVs contain built-in software that allows real-time modifications to preprogrammed routes through external input to avoid potential threats (*e.g.,* ships or sea ice). Using this software, researchers were able to track the movements of a tagged leopard shark (*Triakis semifasciata*) autonomously over several hours using tag transmissions received by a directional hydrophone attached to an AUV (Lotek MAP600RT) as navigational input (Clark et al., 2013). The development of a custom AUV (iSAT) aims to use a similar approach to track large-scale whale shark (Rhincodon typus) movements in the Red Sea while transmitting GPS locations to ARGOS satellites in real time (Llewellyn, 2012). Although the acoustic transmissions of tagged deep-water fish are unlikely to be detected by surface-based hydrophones or receivers (see Section 3.1.1), the operating depth range of some subsurface AUVs (*e.g.,* Slocum glider; 40–1000 m; Teledyne Marine, 2017 Dec 13) would allow tag detection to occur *in situ*.

Acoustic tags deployed on deep-water animals can also be incidentally detected at depth by moored or cabled hydrophones deployed on the seafloor or mid-water column which are intended to record ambient noise in marine environments. These hydrophones, commonly used to listen for seismic activity, for military applications such as submarine detection, or for the monitoring of whales identified by their vocalizations (Mellinger et al., 2007), record sounds across a range of frequencies often including 69 kHz. Cabled hydrophone arrays are expensive to maintain and are primarily employed by governmental agencies such as the military, restricting access to data (Mellinger et al., 2007). However, hydrophone arrays deployed by oceanographic institutes such as NOAA's Hatfield Marine Centre (Autonomous Hydrophone Array (AHA), 2017) and Ocean Networks Canada (Clayoquot Slope High Frequency Hydrophone, 1258m depth; Ocean Networks Canada, 2017 Dec 14) (used primarily to study volcanic and tectonic processes) are not bound by security restrictions, and could provide additional coverage for deep-water acoustic telemetry studies. While it is possible for researchers to decode acoustic tag transmissions and tag IDs by comparing test tag transmissions and their corresponding hydrophone detections, the development of decoding services could integrate tag manufacturers in this novel data process and maintain a cooperative relationship among users.

3.4 Conclusions

The examples highlighted in this review reveal developments in the field of biotelemetry that have facilitated novel studies of deep-water species and which could be used to further advance the monitoring of fish movements in the deep sea. Preliminary studies using custom-built telemetry equipment successfully demonstrated the first *in situ* tagging of abyssal fishes through tag ingestion. Further developments in underwater tagging equipment and improved methodologies for the capture and release of deep-water fish, including underwater tagging and release at depth, have since reduced the effects of physical stressors and improved the survival rates of tagged individuals. Deep-water acoustic telemetry studies have also shown the importance of understanding the spatial ecology of target species for implementing and establishing effective marine management, such as the use of reserves, fisheries management boundaries, and fishery closures. Similarly, satellite tag locations and archival depth and temperature data have provided valuable information on the movement patterns and spawning behaviours of several commercially exploited deep-water teleosts and have elucidated the vertical habitat use, migratory capacity, and potential for population connectivity of several data deficient chondrichthyan species. Future technological adaptations will increase the functional depths and longevity of existing telemetry equipment, extending the depth ranges of telemetry studies and broadening the collection of oceanographic data. Innovative experimental designs coupling telemetry technologies (*e.g.*, linking acoustic, archival and satellites, in addition to gliders and hydrophones) will also improve data retrieval rates and increase the scope of data collected by tagged animals. As resource exploitation efforts extend further into the deep ocean, ecosystem assessments providing the baseline data required to estimate the extent of anthropogenic impacts will be essential to ensure the sustainability of deep-water communities. Continued innovations in telemetry experimental design and data analysis are necessary to facilitate research that will allow appropriate monitoring in the deep sea and to ensure the sustainable exploitation of natural resources in this highly understudied environment.

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TABLES/FIGURES

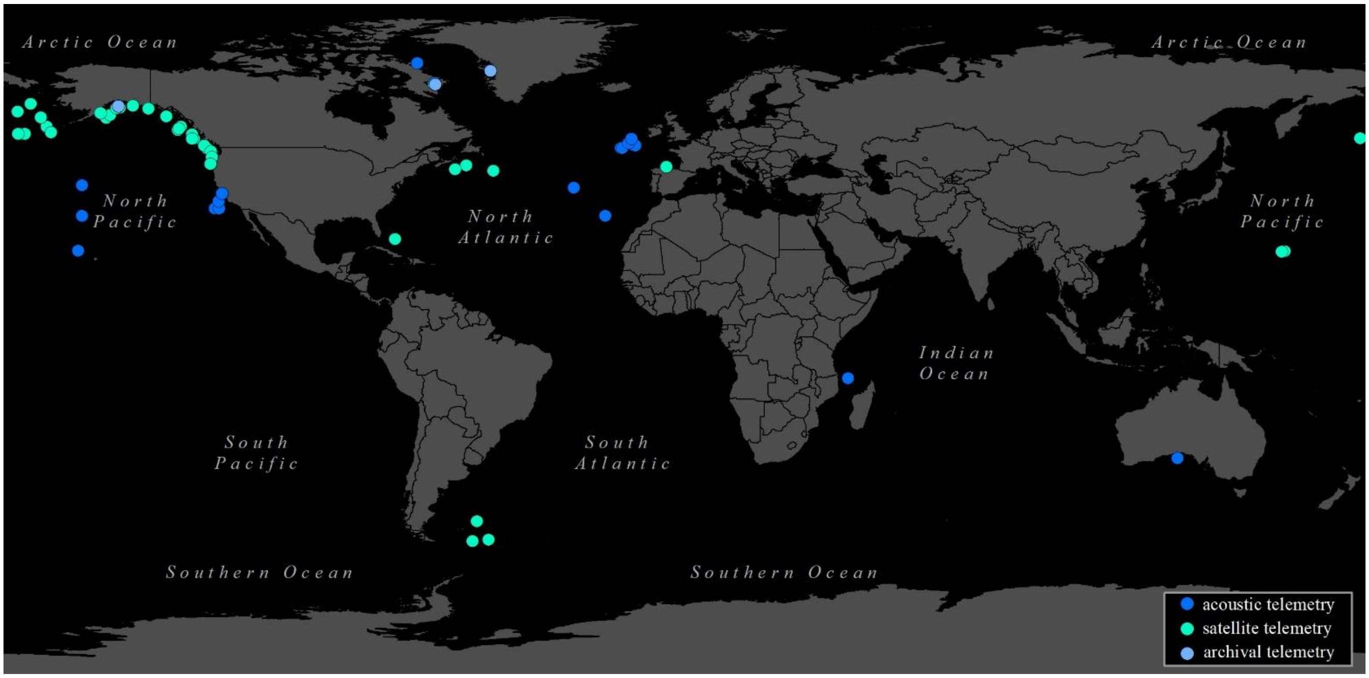

Figure 3.1 | Capture locations of fish tagged in deep-water acoustic (n=22), satellite (n=18), and archival telemetry (n=3) studies published between 1986 and 2018. Due to the vast spatial coverage of individual studies, points represent study sites rather than actual study counts.

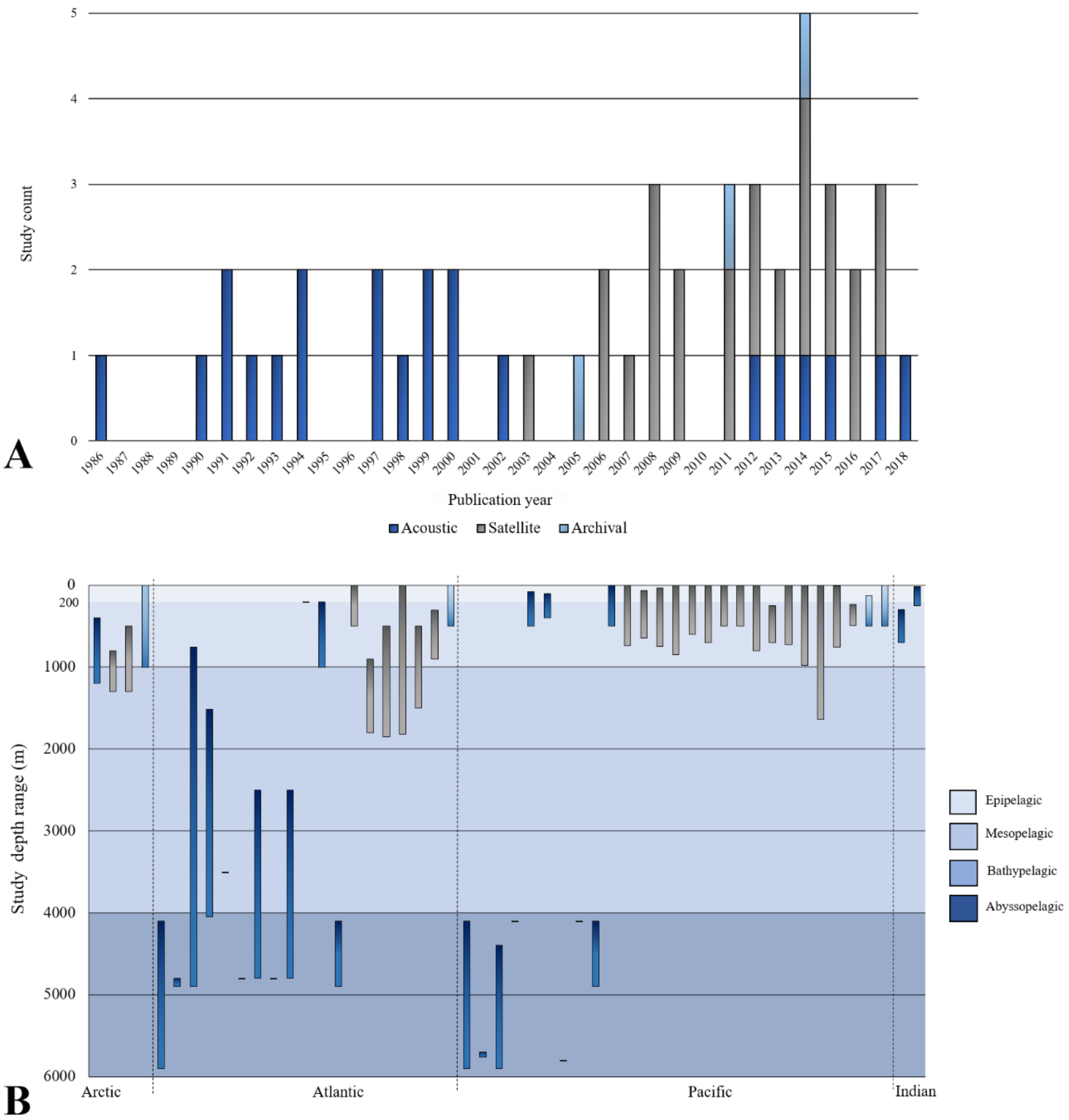

Figure 3.2 | A) Count of deep-water acoustic, satellite, and archival telemetry studies published between 1986 and 2018 by year of publication. B) Depth ranges (m) of animal movement records from reviewed acoustic, satellite, and archival telemetry studies published between 1986 and 2018 arranged by the ocean basin in which tagging and tracking occurred (Arctic, Atlantic, Pacific, Indian). Bar length reflects the range of depths covered by: a) all acoustic receivers or hydrophones in a given study (acoustic telemetry studies), or b) by maximum and minimum depths of animal detections or recorded movements as given in the literature (all study types). Dashed lines show divisions between studies grouped by ocean basin, while bar colour denotes study type, and background colours depict oceanic depth divisions.

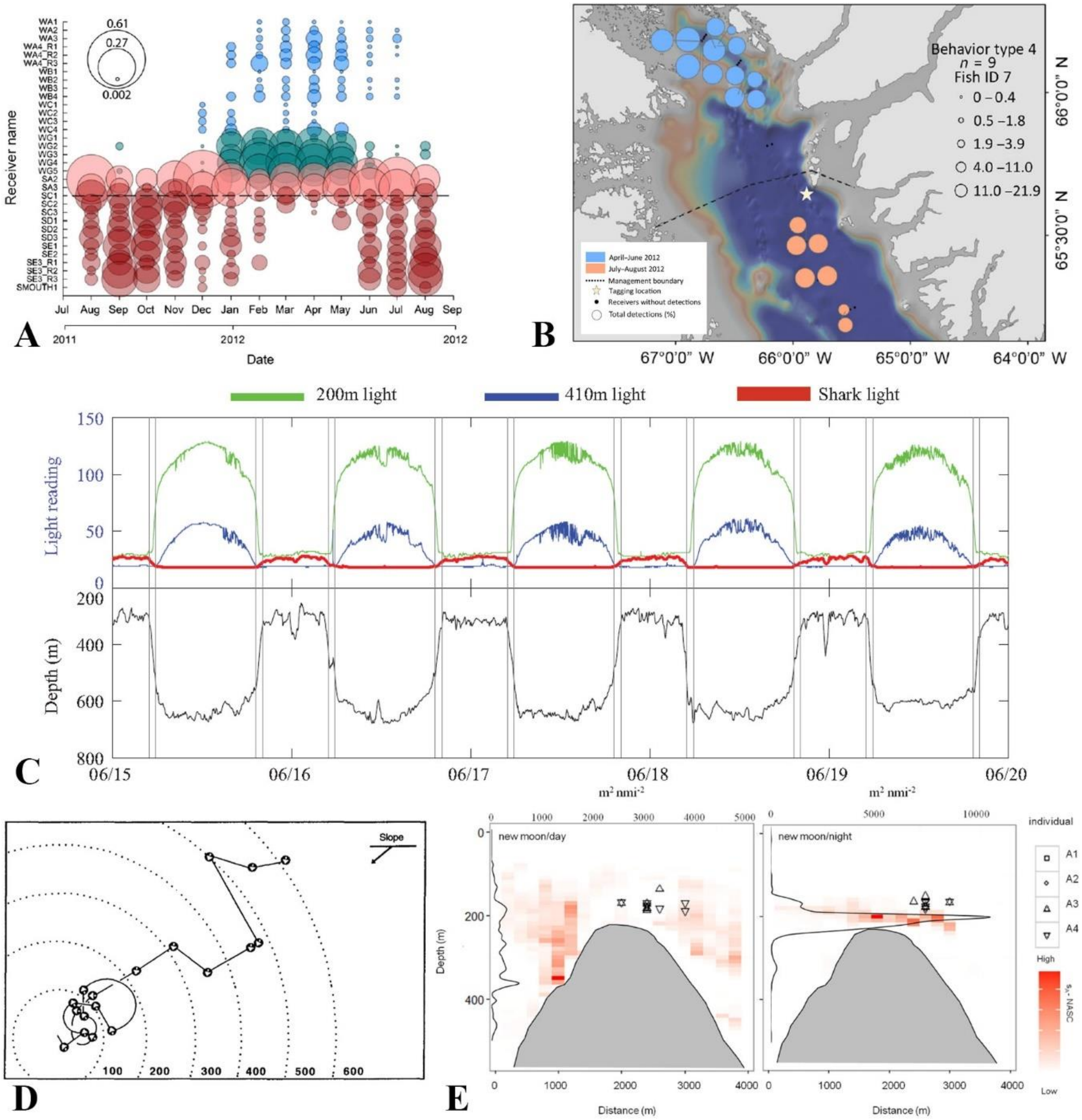

Figure 3.3 | Animal movement records from deep-water telemetry studies: A) From Hussey et al. (2017): Monthly residency index (RI = # of days an individual was detected on a receiver/total days detected across array - shown by circle area) of acoustic-tagged Greenland halibut (*Reinhardtius hippoglossoides*) at specified acoustic receivers within Cumberland Sound, Canadian Arctic (red = deep water region, south of Cumberland Sound Management Boundary [CSMB = dashed line], pink = deep water, north of CSMB, green = gate receivers connecting deep and shallow waters, blue = shallow water, northernmost region. B) From Hussey et al. (2017): Detection profile of Greenland halibut ID 7 detected in >3 regions within Cumberland Sound. Pie charts represent the proportion of detections on unique receivers for 3 time periods, and the size of the pie chart varies depending on the percentage of detections recorded for each receiver over the entire study period, with the data range displayed on the right side of the map. C) From Comfort & Weng (2015): Five

days of light data from MiniPAT tags (Wildlife Computers) moored at 210 m and 410 m on the south Oahu slope, Hawaii alongside concurrent light and depth data from a tagged bluntnose sixgill shark (*Hexanchus* griseus; upper panel) and the vertical movements of the same shark during the same 5 day period (lower panel; vertical grey lines bound the crepuscular period from nautical dawn/dusk to sunrise/sunset). D) From Bagley et al. (1994): Track of a rough abyssal grenadier (*Coryphaenoides armatus*) with a code-activated transponder (CAT) in its stomach measured by Aberdeen University Deep-Ocean Submersible (AUDOS) at a sounding of 3500 m. The centre of the circles is the point of ingestion of the CAT and data points are 15 min apart, except where dropouts occur and the arrows within each data point indicate the current at that time as measured at the AUDOS vehicle. The slope arrow points down the maximum gradient of the local bottom topography determined from charts. E) From Afonso et al. (2014): Vertical movements of four blackspot seabream (*Pagellus boaraveo*) measured by active acoustic telemetry overlaid on the closest echosounder transect collected during the same day/night time period showing potential prey distribution over the west summit of Condor seamount, Azores. Backscatter strength is binned into 106100 m cells with the higher backscatter strength represented by increasingly darker red cell.

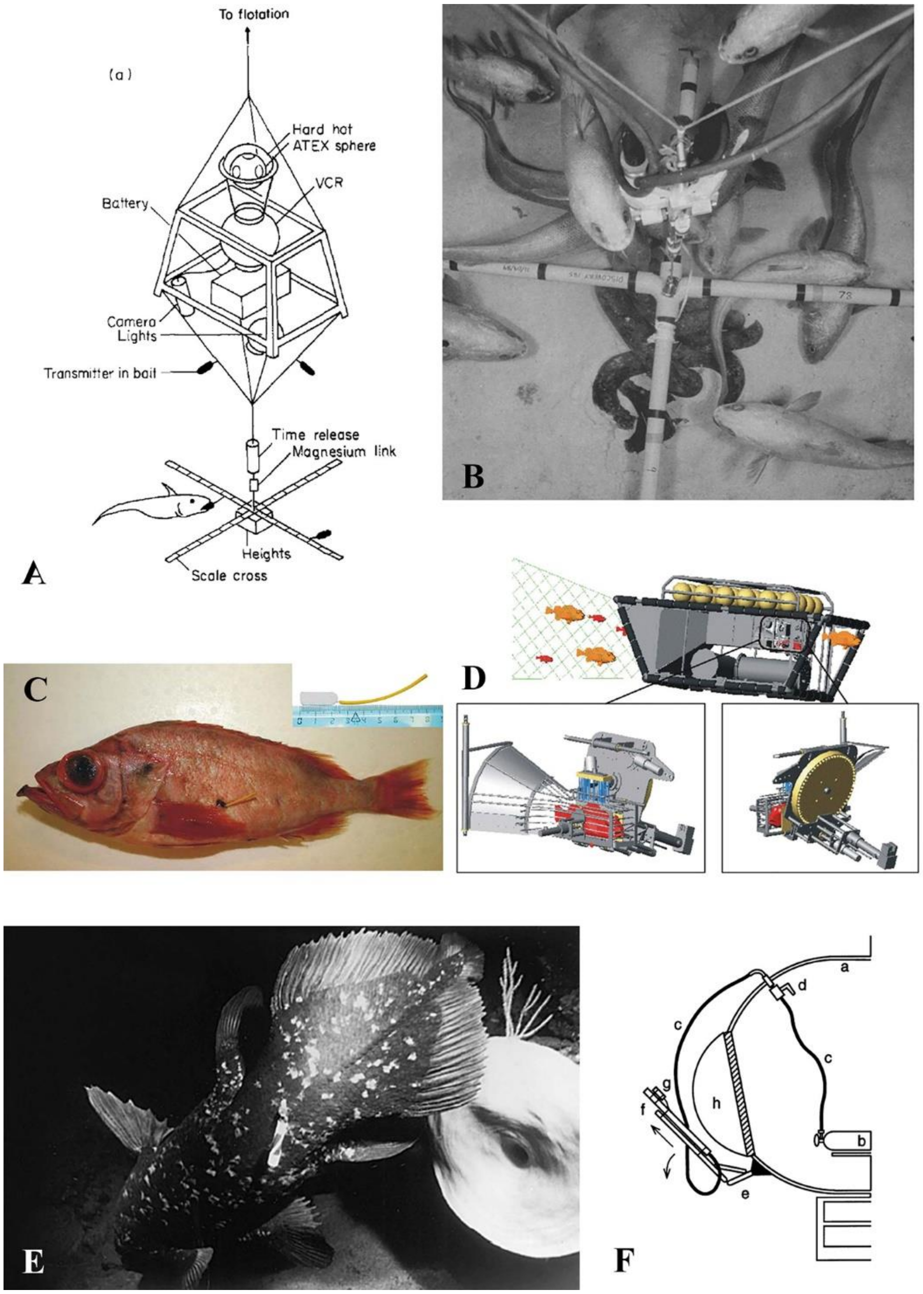

Figure 3.4 | In situ tagging approaches used in deep-water telemetry studies: A) From Priede and Smith (1986): The Free Vehicle Video/Acoustic Tracking Experiment (FVV/ATEX) showing acoustic transmitters wrapped in balls of bait used to remotely tag rough abyssal grenadiers, Coryphaenoides armatus (each arm of the cross is 1m long). B) From Armstrong et al. (1992): Rough abyssal grenadiers attracted by baited transmitters attached to Aberdeen University Deep-Ocean Submersible (AUDOS) at Station PAP (Porcupine Abyssal Plain) (intervals between all black scale marks are 20 cm). C) From Sigurdsson et al. (2006): A recaptured deep-water redfish (Sebastes mentella) tagged using remote underwater-tagging equipment (panel D) and dummy tag. D) From Sigurdsson et al. (2006): Underwater-tagging equipment used to tag deep-water redfish attached to the

cod-end of a trawl net; inserts depict the rear part of a funnel which directs fish into a tagging chamber where it is positioned using hydraulic pumps (viewed from the left, left panel) and the right-side view of the tagging chamber showing the 59-tag magazine. E) From Schauer et al. (1997): Coelacanth (Latimeria chalumnae) with sonic tag deployed via manned-submersible (panel F) foraging along the slopes of Grande Comore. F) From Schauer et al. (1997): Arrangement of component of the pneumatic gun (mounted to a manned submersible) used to remotely tag coelacanths (see reference for full description).

Table 3.1 | Review of deep-water acoustic telemetry studies published between 1986 and 2018. Summarized information includes: i) ocean basin where tagging occurred, ii) species of interest, iii) sample size (number of animals tracked), iv) tag type, v) tag deployment method, vi) tag attachment method, vii) duration of animal tracking, viii) maximum reported detection range of acoustic receivers, ix) vertical depth range of recorded animal movements, and x) the number of deployed tags which were not detected during the tracking study.

Count	Reference	Ocean basin	Species	Sample size	Tag type	Tag deployment method	Attachment type	Tracking duration	Max detection range	Depth range	Tags not detected
1	Priede and Smith (1986)	Mid Pacific	*C. yaquinae*	6	AT	FFV	Ingested	12 - 15 h	NR	5704 - 5763 m	NR
2	Priede et al. (1990)	N Pacific	*C. armatus* and *C. yaquinae*	23	CAT	FFV	Ingested	80 - 277 min	100 - 500 m	4400 - 5900 m	NR
3	Armstrong et al. (1991)	Mid Pacific	*C. yaquinae*	10	AT	FFV	Ingested	16 h	>1000 m	5800 m	NR
4	Priede et al. (1991)	N Atlantic, N Pacific	*C. armatus* and *C. yaquinae*	63	AT	FFV	Ingested	< 24 h	1000 m	4100-5900 m	8
5	Armstrong et al. (1992a)	NE Atlantic	*C. armatus*	21	AT	FFV	Ingested	1 - 23 h	1000 m	4800-4900 m	NR (31 not ingested)
6	Bagley (1993)	N, Pacific, N Atlantic, NE Atlantic	*C. armatus* and *C. coelolepis*	17	CAT	FFV	Ingested	NR	500 m	4100 m, 4900 m, and 757 - 4050 m (4100 - 4900 m overall)	NR
7	Bagley et al. (1994)	NE Atlantic	*C. coelolepis*, *A. rostrata*, and *C. armatus*	16 (11, 2, and 3 resp.)	CAT	FFV	Ingested	3 - 9 h	500 m	1517 - 4050 m	NR
8	Priede et al. (1994)	N Pacific	*C. armatus*	11	CAT, pingers	FFV	Ingested	98 - 150 min	NR	4100 m	NR
9	Bagley and Priede (1997)	NE Atlantic	*C. armatus*	3	CAT	FFV	Ingested	10 h	500 m	3500 m	0

10	Smith et al. (1997)	NE Atlantic	*C. armatus*	8	CAT	FFV	Ingested	110 - 634 min	200 - 500 m	4800 m	2
11	Collins et al. (1998)	NE Atlantic	*C. armatus*	19	CAT	FFV	Ingested	60 - 245 min	500 m	2500–4800 m	2
12	Bagley et al. (1999)	NE Atlantic	*C. armatus*	1	CAT	FFV	Ingested	NR	500 m	4800 m	NR
13	Collins et al. (1999)	NE Atlantic	*C. armatus*, *A. rostrata*	10 (4 and 6 resp.)	CAT	FFV	Ingested	up to 120 min	500 m	2500-4800 m	NR
14	Hissmaan et al. (2000)	W Indian	*L. chalumnae*	9	VCAT and pingers	*In situ* tagging via submersible	Dart	11-146 h	1000 m	16-253 m	2 (tags fell off prematurely)
15	Starr et al. (2000)	NE Pacific	*S. chloristictus* and *S. paucispinis*	22 (6 and 16 resp.)	VCAT	Capture and release	Underwater surgical implantation	1-140 d	~800 m	200 m	0
16	Starr et al. (2002)	NE Pacific	*S. chloristictus* and *S. paucispinis*	22 (6 and 16 resp.)	VCAT	Capture and release	Underwater surgical implantation	1-140 d	~800 m	200 m	0
17	Afonso et al. (2012)	NE Atlantic	*P. bogaraveo*	28	VCAT	Capture and release	Surgical implantation	829 d	600 m	~200 m	NR
18	Weng (2013)	Mid Pacific	*E. coruscans*, *E. carbunculus*, and *P. filamentosus*	85 (65, 17, and 3 resp.)	VCAT	Capture and release	Surgical implantation	~28 - 40 d	NR	100 - 400 m	44 (35, 7, and 2 resp.)
19	Afonso et al. (2014)	NE Atlantic	*P. bogaraveo*	8	VCAT	Capture and release	Surgical implantation	48 - 72 h active, 22 mos. passive	450 m	200 - 1000 m	NR
20	Daley et al. (2015)	Indian	*C. zeehaani*	71	VCAT	Capture and release	Fin mount	488 d	650 - 900 m	300 - 700 m	9 not detected

21	Hussey et al. (2016)	Arctic	*R. hippoglossoides*	223	VCAT	Capture and release	Surgical implantation	12 - 24 mos.	273 - 802 m	400 - 1200 m	56 not detected
22	Barkley et al. (2018)	Arctic	*R. hippoglossoides*	66	VCAT	Capture and release	Surgical implantation	12 mos.	NR	>100-800 m	44 not detected

*Species names: *Coryphaenoides yaquinae*, *Coryphaenoides armatus*, *Centroscymnus coelolepis*, *Antimora rostrata*, *Latimeria chalumnae*, *Sebastes chloristictus*, *Sebastes paucispinis*, *Pagellus bogaraveo*, *Etelis coruscans*, *Etelis carbunculus*, *Pristipomoides filamentosus*, *Centrophorus zeehaani*, and *Reinhardtius hippoglossoides*
**Tag types: passive acoustic pinger, AT = acoustic transponder, CAT = code activated acoustic transponder, VCAT = VEMCO coded acoustic transmitter
***Tag deployment methods: FFV = Free-Fall Vehicle
****NR = information not reported.

Table 3.2 | Review of deep-water satellite telemetry studies published between 2003 and 2018. Summarized information includes: i) ocean basin where tagging occurred, ii) species of interest, iii) sample size (number of animals tracked), iv) tag type, v) tag attachment method, vi) duration of animal tracking, vii) vertical depth range of recorded animal movements, viii) number of proposed tag failures, and ix) number of proposed pre-mature tag releases (resulting in incomplete datasets).

Count	Reference	Ocean basin	Species	Sample size (tag datasets used/tags deployed)	Tag type	Attachment type	Tracking duration	Depth range	Prop. tag failures	Prop. premature releases
1	Seitz et al. (2003)	NE Pacific	*H. stenolepis*	8/14	PAT	Dart	133 - 670 d	2 - 502 m	5	NR
2	Loher and Seitz (2006)	NE Pacific	*H. stenolepis*	10/12	PAT	Dart	23 d	0 - 736 m	0	2
3	Seitz et al (2007)	N Pacific	*H. stenolepis*	9/12	PAT	Dart	12 - 258 d	<65 - >650 m	3	1
4	Seitz et al (2008)	N Pacific	*H. stenolepis*	16/25	PAT	Dart	193 - 206 d	32 - 748 m	9	0
5	Loher (2008)	NE Pacific	*H. stenolepis*	31/48	PAT	Dart	365 d	0 -848 m	6	8
6	Loher and Seitz (2008)	NE Pacific	*H. stenolepis*	72/102	PAT	Dart	213 - 365 d	0 - 600 m	NR	NR

7	Loher and Blood (2009)	NE Pacific	*H. stenolepis*	57/78	PAT	Dart	182 - 213 d	0 - 699 m	NR	11
8	Loher and Clark (2009)	NE Pacific	*H. stenolepis*	78/115	PAT	Dart	11 - 380 d	0 - >500 m	8	28
9	Loher (2011)	NE Pacific, NW Atlantic	*H. stenolepis*	94/138 PAT, 13/166 archival	PAT, archival	Dart (PAT), surgical implantation & dorsal mount (archival)	≤ 365 d (PAT), ≤ 1095 d (archival)	0 - 500 m	NR	NR
10	Seitz et al. (2011)	NE Pacific	*H. stenolepis*	55/98	PAT	Dart	165 - 240 d	0 - 800 m	11	4
11a	Peklova (2012)	Arctic	*R. hippoglossoides*	9/9	PAT	Dart	40-300 d	800-1300 m	0	0
11b	Peklova (2012)	Arctic	*A. hyperborea*	7/9	PAT	Fin mount	40-300 d	500-1300	2	4
12	Brown et al. (2013)	SW Atlantic	*D. eleginoides*	17/30	PAT	Dart	1 - 180 d	900 - 1800 m	8	15
13	Rodríguez-Cabello and Sánchez (2014)	NE Atlantic	*C. squamosus*	4/5	PAT	Dorsal anchor	130 d	496 -1848 m	1	0

14	Campana et al. (2015)	NW Atlantic	*S. microcephalus*	14/15	PAT	Dart	35 - 334 d	0 - 1816 m	1	4
15	Comfort and Weng (2015)	N Pacific	*H. griseus*	4/6	PSAT and VCAT	NR	53 - 97 d	250 - >700 m	1	0
16	Rodríguez-Cabello et al. (2016)	NE Atlantic	*C. squamosus*	8/9	PSAT	NR	45 - 121 d	500 - 1500 m	1	2
17	Shipley et al. (2017)	NW Atlantic	*S. cubensis*	7/8	PSAT	Fin mount	5 - 14 d	304 - 904 m	1	NA

*Species names: *Hippoglossus stenolepis, Reinhardtius hippoglossoides, Amblyraja hyperborea, Dissostichus eleginoides, Centrophorus squamosus, Somniosus microcephalus, Hexanchus griseus*, and *Squalus cubensis*
**Tag types: PAT = pop-up archival tag, PSAT = pop-up satellite archival tag, VCAT = VEMCO coded acoustic transmitter
***NR = information not reported.

Table 3.3 | Review of deep-water archival telemetry studies published between 2006 and 2018. Summarized information includes: i) ocean basin where tagging occurred, ii) species of interest, iii) sample size (number of animals tracked), iv) tag type, v) tag attachment method, vi) duration of animal tracking, vii) vertical depth range of recorded animal movements, and viii) number of proposed tag failures.

Count	Reference	Ocean basin	Species	Sample size (tag datasets used/tags deployed)	Tag type	Attachment type	Tracking duration	Depth range	Prop. tag failures
1	Seitz et al. (2005)	NE Pacific	*H. stenolepis*	2/14	PAT	Dart	135-155 d	126 - 502 m	NR
2	Loher (2011)	NE Pacific & NW Atlantic	*H. stenolepis*	13/166 (12 LTD1300, 1 Mk9 recovered)	Archival (LTD1300 and Mk9)	Dorsal mount, sugical implantation	< 1095 d	0 - 500 m	NR
3	Boje et al. (2014)	Arctic Ocean	*R. hippoglossoides*	12/210	Archival (DST milli)	Dorsal mount	69 - 176 d	0 - 1000 m	1

*Species names: *Hippoglossus stenolepis,* and *Reinhardtius hippoglossoides.*

**Tag types: PAT = pop-up archival tag, Mk9 = archival tag manufactured by Wildlife Computers, LTD1300 = archival tag manufactured by Lotek Wireless, DST milli = archival tag manufactured by Star Oddi.

***NR = information not reported.

Table 3.4 | Definitions of data categories extracted from deep-water acoustic, satellite, and archival telemetry studies.

Data category	Relevant telemetry class	Definition
Tracking duration	Acoustic, satellite, & archival	Also referred to as 'time at liberty'. Reported as a range between the minimum and maximum number of days at liberty reported for all tagged animals within that study. For satellite studies in which days at liberty were not reported, tracking duration was estimated as the time interval between the date of fish tagging and the programmed release date of the satellite tags.
Maximum detection range	Acoustic	Reported as either the absolute, approximate, maximum distance of detection, or nominal maximum range. In most of the reviewed studies, maximum detection range was reported as an approximation of the absolute maximum distance (metres) from a receiver wherein a tag's signal could still be detected (Kessel et al., 2014).
Range test	Acoustic	Test conducted in the study environment to determine detection range and to assess the rate and reliability of tag detection relative to environmental conditions that vary across space and time (e.g., salinity, temperature, suspended particles, and water movement) (Medwin and Clay, 1997; Kessel et al., 2014; for further detail see Section 3.2.1).
Depth range	Acoustic, satellite, & archival	Describes the vertical limits of the movements of each species recorded during a study (metres) as determined by the minimum and maximum depths recorded across all tagged individuals per study.

CHAPTER 4

Seasonal residency and movement behaviours of Greenland sharks (*Somnious microcephalus*) in a coastal Arctic fjord

4.1 Introduction

The movement behaviours of individual organisms contribute fundamentally to larger ecological patterns in population and community dynamics and species-level adaptation to environmental change (Dingle, 2014). These movements occur across a range of spatial and temporal scales which ultimately dictate the degree to which individuals interact with, and therefore influence their environments (Morales et al., 2010). Scales of movement also vary widely among species, from those that have relatively restricted home ranges and may be highly site attached (*e.g.,* anemonefishes; *Amphiprioninae,* and sloths; *Bradypodidae*), to those that can traverse large expanses of the globe, extending the breadth of their geographic ranges across thousands of kilometers (*e.g.,* albatrosses; *Diomedeidae*, and baleen whales, *Balaenopteridae*). For many species, however, these behavioural archetypes are not mutually exclusive. The scales of movement exhibited by individuals can vary drastically between life stages or even by season (Grubbs, 2010). In many cases, periods of predominantly transient behaviour or alternatively, site attachment, may be broken up by long-distance directed movements and bouts of seasonal residence in specific locations associated with reproduction or feeding. The potential for pronounced shifts in both movement and distribution to occur within an individual’s lifespan can have critical implications for species management, as the importance of certain habitats may vary over time and individuals may not be restricted to spatially-designated protected areas at all life stages (Grüss, Kaplan, Guénette, Roberts, & Botsford, 2011). These considerations emphasize the need for long-term studies that can capture the complete range of individual movement behaviours to understand their effects on the overall population.

Biotelemetry devices have allowed researchers to observe and measure animal behaviours indirectly and from remote locations (Cooke et al., 2004; Hussey, Kessel, et al., 2015; Lennox et al., 2017). In relatively obscure environments (*e.g.*, deep water), or those that can be seasonally inaccessible (*e.g.*, seasonally ice-covered polar regions), telemetric devices provide unique opportunities for researchers to observe animal behaviours as they occur throughout the year and *in situ*. At present, studies of marine animal movements use methods such as satellite and acoustic telemetry to observe behaviours that typically occur over periods of weeks to months, with the longevity of monitoring dictated by factors such as tag lifespan (imposed by battery life, tag size, or memory capacity) and tag retention by the host (Donaldson et al., 2014; Hussey, Kessel, et al., 2015; Jepsen, Thorstad, Havn, & Lucas, 2015). While this duration may be sufficient for observing shifts in movement and distribution taking place over brief time periods, they are unlikely to capture the complexity of movement patterns that occur gradually over much longer timespans. This is particularly relevant for studies in which highly mobile marine species are monitored using spatially restricted telemetry techniques such as static acoustic telemetry. In this case, where tagged animals are free to leave and enter the study area at will, long-term observation may be essential for detecting infrequent behaviours such as the periodic recurrence of individuals in specific regions (Lowe, Wetherbee, & Meyer, 2006; March, Palmer, Alós, Grau, & Cardona, 2010; Reubens, Pasotti, Degraer, & Vincx, 2013). Furthermore, the stress of animal capture and tagging presents potential confounding factors for short-term movement studies. Animal behaviour following release from tagging may not be representative of natural behaviours (Block, Booth, & Carey, 1992; Campana, Joyce, & Manning, 2009; Hoolihan et al., 2011), however, without either high-resolution data or long-term monitoring it can be difficult to determine the nature or degree of severity of this effect (Whitney et al., 2016). Importantly, multi-year observations provide the opportunity to examine both post-release behaviour and natural return events over ecologically relevant timescales.

Long-term telemetry studies can be particularly crucial for the study of long-lived species, particularly those that display high mobility. As the world’s longest-lived vertebrate (Nielsen et al., 2016), the Greenland shark (*Somniosus microcephalus*) represents one such species. Greenland sharks exhibit the slowest observed mean swim speed (0.34 ms^{-1}) and tailbeat frequency (0.15 Hz) relative to their size of any fish species (Watanabe et al. 2012). Yet despite this fact, they are highly mobile (Campana, Fisk, & Peter Klimley, 2015; Fisk, Lydersen, & Kovacs, 2012) and broadly distributed throughout coastal and offshore Baffin Bay (Eastern Canadian Arctic). As the only shark species inhabiting the periodically ice-covered regions of the North Atlantic (McMeans et al., 2013), they face extreme temperatures and dramatic seasonal fluctuations in light levels and productivity (Gradinger, 1995). In addition, Greenland sharks comprise one of the primary bycatch species for commercial and community-level Arctic fisheries and are vulnerable to capture throughout the year across both deep-water and inshore habitats (Davis et al. 2013). While considered to occupy a high trophic level in Arctic marine food webs (Fisk, Tittlemier, Pranschke, & Norstrom, 2002; Hussey et al., 2014), their ecological role and various aspects of their life history, physiology, and behaviour remain largely unknown. For example, past telemetry studies have primarily relied on short-term methods such as archival satellite telemetry or active acoustic tracking to examine Greenland shark movements. While this work has provided important insights into our understanding of vertical movement behaviours and revealed this species' capacity to undertake large-scale horizontal displacements, the use of these methods has required the sacrifice of either data resolution or monitoring duration (Edwards et al., 2019b). Consequently, the significance of observed movement behaviours relative to this species' extremely prolonged lifespan is difficult to ascertain.

Static acoustic telemetry is the only technique currently available for conducting long-term animal movement studies in marine environments and is providing valuable ecological data for a number of deep-water and Arctic fish species (Edwards, Pratt, Tress, & Hussey, 2019). The use of receivers fixed to the seabed and long-lifespan transmitters (up to 10 y) allows tagged individuals to be detected over multiple years, producing temporally replicated detection datasets for large numbers of tagged individuals. These datasets can then be analysed in relation to corresponding environmental records (Donaldson et al., 2014; Heupel et al., 2015) and used to determine behavioural variation over ecologically relevant time frames. This multi-year approach has thus far revealed temporal variability in residency (Cagua et al., 2015; Huveneers, Harcourt, & Otway, 2006; O'Toole et al., 2011; Pillans et al., 2014), and habitat use (Afonso, Graça, Berke, & Fontes, 2012; Carlson, Heupel, Bethea, & Hollensead, 2008; Munroe, Simpfendorfer, & Heupel, 2014) in marine and freshwater ecosystems and is becoming a popular tool for assessing the efficacy of Marine Protected Areas and other spatially designated management approaches (Heupel et al., 2015; Lea, Humphries, von Brandis, Clarke, & Sims, 2016; Tinhan et al., 2014).

The occurrence of Greenland sharks in the coastal fjord systems of the Eastern Canadian Arctic has been observed by both scientific surveys and Inuit community fisheries, for whom the incidental bycatch of this species poses problems (Hussey, Cosandey-Godin, et al., 2015; Idrobo & Berkes, 2012; Walsh, 2018; Wheeland & Devine, 2018). Despite the regularity of these encounters, an understanding of how and when sharks use these environments has yet to be established. In the current study, we used a large-scale static acoustic telemetry array to examine the movement behaviours of 65 tagged Greenland sharks within a model deep-water Arctic fjord system and region of current fishery development (Scott Inlet, Nunavut) over a period of 6 years. Specifically, individual detection records were used to address key questions concerning patterns in coastal residency (*e.g.*, timing and duration), inshore-offshore connectivity, and fine-scale movement behaviours (*e.g.*, use of deep-water channels, core and general home ranges) for this data-deficient species. The repeated detection of individuals across multiple years allowed the comparison of behaviours recorded in both post-tagging (*i.e., disturbed*) and return-year (*undisturbed*) detection periods, allowing examination of potential post-release behavioural modification in a large mobile species. Shark presence and absence in the fjord were then compared to environmental variables sampled throughout this highly dynamic region to determine the drivers of residency in coastal waters. These data provide the first glimpse into spatiotemporal variability in the use of coastal habitats by this species and will improve our ability to predict how climate change and increased fishing pressure in Arctic regions could affect Greenland shark populations in the future.

4.2 Methods

4.2.1 Study site

Tagging and acoustic monitoring of Greenland sharks took place in the Scott Inlet fjord system, situated on the northeastern coast of Baffin Island, Nunavut (Canada; 71°15' N, 70°30' W; **Fig. 4.1**). The study system is composed of two deep-water fjords (Scott Inlet and Sam Ford fjord) which have depths ranging from 600-800 m at their centre and are connected to offshore waters by a prominent channel (800 m depth at its midpoint; Barkley, Hussey, Fisk, Hedges, & Treble, 2018). The study site is also characterized by a high degree of seasonality, alternating between periods of open water (mid-August to early October) and complete coverage by land-fast sea-ice (mid-October to early August). Importantly, the inlet is also the proposed location for the development of a winter Greenland halibut (*Reinhardtius hippoglossoides*) fishery for the community of Clyde River (Walsh, 2018).

4.2.2 Shark tagging and acoustic monitoring

The Scott Inlet array (ASI) was composed of 54-77 acoustic receivers (VR2W and VR4; VEMCO, Bedford, NS, Canada) deployed at depths between 134 and 823 m and arranged into two array designs. In 2013, 54 receivers were deployed approximately 1 km apart in a series of gates (a linear arrangement of closely spaced receivers; gates G01-G07; **Fig. 4.1**) spanning perpendicularly across the deep-water channels of the fjords. The proximity of receivers within each gate was chosen based on the results of range tests conducted in a similar Arctic basin (*i.e.*, Cumberland Sound; Hussey et al., 2017) to maximize detection efficiency. The high probability of detecting fish transiting through the gates allows the examination of movements between the various regions of the fjord system (*e.g.,* the inner sections of the fjords and the central basin), as well as transitions between coastal and offshore waters via the main deep-water channel. These coastal/offshore transitions in turn provide a proxy for identifying temporal patterns in coastal residency.

In 2014, an additional 23 receivers were deployed in a series of gates which form a grid-like array across the system's central basin (gates G08-G14; **Fig. 4.1**). The grid array design was deployed to detect if sharks enter the system via routes other than the main deep-water channels and to allow a more detailed examination of fine-scale movements and habitat use in the proposed fishing area.

Receivers were deployed on moorings composed of two nylon rope risers anchored by a cast-iron disc and suspended by a subsurface float. Mooring retrieval was facilitated by the use of an acoustic release mechanism (PORT MFE; EdgeTech, West Wareham, MA, USA) which, when activated by signals sent using a cabled hydrophone, detached itself and the upper portion of the mooring (float, upper riser with equipment) from the anchor, allowing the equipment to float to the surface. Following their initial deployment, all receivers were retrieved annually for servicing and the acquisition of archived detection data before being redeployed at their original locations.

Greenland sharks were captured during September and October (2013-2016) using bottom longlines (~735 m length) set at depths between 300 and 900 m for 12 h. Size 16 and 17 Tuna circle hooks baited with frozen squid were attached to 50 x 1.5 m steel leader gangions spaced 5.5 m apart along the length of each longline. Upon capture, sharks were removed from hooks and held alongside a Zodiac using ropes and sling-straps for the tagging procedure. Using standard surgical procedures, 69 kHz acoustic transmitters (V16-6x, V16-TP-4x; VEMCO Ltd., Halifax, Nova Scotia) were inserted through a small incision made on the animal's ventral side (anterior to the pelvic fins and just off the midline) which was then closed using 3-4 interrupted sutures. The tagging process for each shark, including biological sampling (blood, fin clips) and measurement (total length [L_T; m]) took ~10 min. Tagged sharks were then released at the capture location and monitored to ensure normal swimming behaviour (see **Fig. 4.1** for release locations).

4.2.3 Data analysis

Greenland shark detections were summarized and visualized using the statistical software R v.3.5.3 (R Core team, 2019) and the packages, *tidyverse* (Wickam, 2019) and *ggplot2* (Wickam, 2016). Maps were produced using ArcMAP (Esri Inc., 2019).

4.2.3.1 Coastal residency

The timing of and duration of annual Greenland shark residency in Scott Inlet was first examined by visualizing daily detections for all individuals across the entire study period (Sept. 2013 – Sept. 2018; **Fig. 4.2**). Based on the intermittent presence of tagged sharks in the system, individual detection profiles were then broken into two categories. The first category of detections, hereby referred to as *disturbed* events, encompasses the period of residency following an individual's release directly after tagging, up until its final exit from the system before a prolonged period of absence (>60 d). As shark capture and tagging occurred within the fjord, these *disturbed* events are characterized by the fact that the actual date of a shark's entry into the system prior to tagging is not known and therefore the residency parameters calculated for this period are not comparable to those of natural re-entry events. Furthermore, because this period occurs immediately after the tagging event, whereby the animal is subjected to a brief period of elevated stress, behaviours exhibited during the post-release residency period (*i.e.*, the first 24 hours; Watanabe et al. in review) may not be reflective of the animal's natural behaviours. In contrast, periods of natural re-entry into the system by previously tagged sharks in subsequent calendar years were classified as *undisturbed* events. In these instances, where both the dates of entry into and exit from the system are known, analyses of residency are representative of the total duration of annual Greenland shark presence in Scott Inlet.

To further quantify Greenland shark residency during *disturbed* and *undisturbed* events, detection span (DS) was recorded as the number of days between an individual's first and last detections in the system prior to a period of extended absence (>60 d). Detection days (DD) are also reported as the number of days during which an animal was detected by any receiver in the array within each detection span. Comparisons of DS and DD across detection years were conducted using the Kruskal-Wallis rank sum test. Differences based on shark sex and size (L_T) were examined using the Wilcoxon rank sum test and Spearman's rank correlation, respectively. After dividing sharks into two length-based age classes (juveniles <2 m L_T, subadults ≥2m L_T; as described by Hussey, Cosandey-Godin, et al., 2015), differences in DS and DD were also compared used the Wilcoxon rank sum test.

Due to the absence of the grid portion of the receiver array in 2013 when the first cohort of tagged sharks were released into the fjord, residency analyses for all *disturbed* events were conducted using only detections archived by moorings present across all monitoring years (G01-G07; **Fig. 4.1**). However, as the timespan of *undisturbed* detections covers only years after the deployment of the grid receivers, detections from the entire array (*i.e.*, both gates and grid receivers) were included in the corresponding analyses.

Entry and exit dates were defined as the dates of the first and last detections within a given year for each tagged shark and were compared among *disturbed* and *undisturbed* detection years for all individuals. Median entry and exit dates were calculated by first transforming all detection dates into the ordinal date (*i.e.*, day-of-year) format and by determining the corresponding calendar date range using the Day of Year Calendar available online via the National Snow & Ice Data Center (https://nsidc.org/data/tools/doy_calendar.html).

4.2.3.2 Use of deep-water channels

The location of each exit event was denoted by the receiver gate on which the event was detected, and the number of exit events were compared across gates to assess the importance of deep-water channels for directing movements between the coastal system and offshore waters. Similarly, for re-entry years, the location (gate) of each animal's first detection in the array following a period of extended absence (>60 d) was noted and the number of entry events was compared across receiver gates.

To examine the influence of cross-sectional channel depth on Greenland shark movement, the total number of individuals detected by each receiver station was calculated for the 7 primary receiver gates (G01-G07). The number of detected individuals was then compared to the mean bottom depth calculated for each receiver across its period of active deployment. The purpose of this comparison was to determine whether tagged Greenland sharks appear to preferentially transit along the deepest part of the fjord's channels, or whether they are more frequently detected in shallower waters, moving along the banks of the deep-water channels.

4.2.3.3 Home range size and location

Home range estimations were calculated using the lattice-based density estimator, *latticeDensity* (Barry & McIntyre, 2011), in the statistical software, R (R Core team, 2019). This method was chosen over standard kernel density estimators due its ability to account for irregular boundaries and 'holes' (*i.e.,* islands), such as those present in our complex study region. Using this method, animal relocations are interpolated over a network of interconnected nodes that form a lattice over the entirety of the study region but can be modified to remove islands and other defined boundaries. This approach is a modification of the standard kernel estimators which do not respect irregular boundaries or holes, often leading to overlap between regions of estimated animal activity and parts of the study area which are, in fact, inaccessible to the tagged animals. To achieve the number of detections required for home range estimation, Greenland shark detections were compiled into groups based on characteristics such as the sex or age-class (juvenile/subadult) of tagged individuals, or by detection period (*disturbed/undisturbed*).

4.2.3.4 Potential drivers of Greenland shark presence/absence

A generalised linear mixed effect model (GLMM) was used to assess the significance of several biological and environmental factors on the detection-based daily presence/absence of Greenland sharks in the ASI acoustic array throughout a portion of the defined study period (Sept 19th, 2014 – Sept 27th, 2018). This time period was chosen to ensure array standardization across years by including only detections recorded after the deployment of the complete array in 2014. Prior to running the model, a correlation matrix was created using the package *corrplot* in R (Wei & Simko, 2017) to identify potential relationships between covariates, allowing the omission of covariates predicted to add bias to the model results.

Shark ID was included as a random effect while fixed effects included two biotic factors, the sex and age-class (juvenile/subadult) of the tagged individual, and three abiotic factors, daily percent sea-ice cover (% cover across the entire array area), daily temperature at the approximate depth of the acoustic receivers (ºC; mean sensor depth = 789 ± 16.08 m), and lunar illumination (% maximum illumination). Lunar illumination is here used as a proxy for tidal cycles which produce changes in the ambient pressure at depth, in addition to the proposed influence of tidal/lunar cycles on monthly shark abundance as observed by the Pangnirtung Inuit in the Cumberland Sound community fishery (Idrobo, 2008).

Weekly percent ice cover was obtained from the Canadian Ice Service archive (data available online at: https://www.ec.gc.ca/glaces-ice/). Temperature data was obtained from sensors deployed on mooring stations at approximately 2 m above the depth of the acoustic receiver. The sensor with the longest continuous temperature record was chosen for inclusion in the model to maintain continuity in the location of temperature records over the duration of the study period (sensor ID: G0902_7703, deployed on station G09-02). Records from this sensor spanned from Sept. 19th, 2014 to Oct. 5th, 2018, with a gap between Sept. 11, 2016 and Oct. 3rd, 2017 during which time no temperature data were available. Historical records of percent lunar illumination were obtained for the nearest community, Clyde River, Nunavut (data available online at: https://www.timeanddate.com/moon/canada/clyde-river). To maintain a consistent number of records for each fixed effect, a total of 4,484 records (days) were excluded from the model dataset. Excluded records included those for which no temperature or lunar illumination data were available.

For shark presence/absence, a tagged shark was determined to be present in the system on any day during which it was detected by any receiver in the ASI array (denoted in the model by a value of 1). For all days during which a shark was not detected by a receiver in the array, the individual was presumed to be absent and was assigned a value of 0. It should be noted that, in several instances, tagged sharks remained undetected for variable amounts of time following detection by one of the innermost gates (G03 & G04) prior to being detected once again by receivers in one of these 2 gates. These periods presented a potential bias in our model, as individuals are known to be present within the interior of the fjord during this time but remain undetected due to the lack of receiver coverage in this area. To correct this issue, such periods of 'apparent absence' between subsequent detections on gates G03 or G04 (hereafter referred to as *'apparent absence periods'*) were identified for all individuals and the days falling within these periods were assigned a value of 1.

Apparent absence periods of >1 d between subsequent detections on gates G03 and G04 were identified for 6 tagged individuals, ranging in duration from 1-56 d (mean and SD = 11.06 ± 13.48). During these periods, sharks remained undetected due to a lack of receivers in the fjord's interior but are known to have been present within the fjord.

Apparent absence periods occurred exclusively during *undisturbed* detection years for all 6 sharks and took place between the months of July and October.

4.3 Results

A total of 65 Greenland sharks (41 males, 24 females [mean L_T = 2.48 ± 0.50 m]), tagged over 4 years (Sept. 18th, 2013 to Sept. 22nd, 2016), were detected in Scott Inlet between Sept. 20th, 2013 and Sept. 27th, 2018 (**Table 4.1**). Of these sharks, 19 were tagged in 2013 (29% of total), 23 in 2014 (35% of total), 8 in 2015 (12% of total), and 15 in 2016 (23% of total). Sharks were classified based on total length (L_T) as either juveniles (<2 m L_T, *n=17*) or subadults (≥2 m L_T, *n=48*), as defined by Hussey et al. (2015). Over the complete study period (2013-2018), a total of 15,094 detections were recorded across the entire array, with an annual mean of 2,516 ± 1,364 (3,385 ± 710 for tagging years [2013-2016] and 778 ± 207 for non-tagging years [2017-2018]).

4.3.1 Coastal residency

4.3.1.1 Timing and duration

In *disturbed* detection years, sharks were detected as early as September 14th-15th (*ordinal date* = 258; date range is used to account for the 2016 leap year) and remained in the fjord until as late as Nov. 21st-22nd (*ordinal date* = 326). Across all *disturbed* detection years, the median date of first detection following tagging was Sept. 30th-Oct. 1st (*ordinal date* = 274) and the median date of exit from the fjord was Oct. 8th-9th (*ordinal date* = 282). Greenland sharks were typically detected on one of the 7 main receiver gates (G01-G07) within a mean of 4.89 ± 5.89 days following tagging.

In *undisturbed* years, sharks were present as early as July 21st-22nd (*ordinal date* = 203) and stayed as late as Oct. 29th-30th (*ordinal date* = 303). The median entry date for sharks returning to the fjord in *undisturbed* years was between August 9th-10th (*ordinal date* = 222) and the median date of departure was Oct. 4th-5th (*ordinal date* = 278).

These results demonstrate a high degree of overlap in the timing of shark presence across both *disturbed* and *undisturbed* (*i.e.,* tagging and re-entry) detection years, with median exit dates differing by only 4 days. However, as tagging typically took place near the end of the ice-free period (late September to early October), detection spans recorded during *disturbed* periods represent only the latter portion of the full period of seasonal residency demonstrated by those reported for *undisturbed* years (**Fig. 4.2**). Overall, Greenland sharks were only detected in the fjord between late July and early November across all study years.

4.3.1.2 Timing of Greenland shark detections relative to environmental variation and lunar cycles

Over the study period, the timing of sea-ice break-up and reformation followed a highly predictable trend, with monthly means of 88-99% cover (*SD* = 0.29-12.74%) observed between November and June and monthly means of 2-57% cover (*SD* = 0.00-28.90%) recorded between July and October across study years (**Fig. 4.2a**). Trends in temperature at depth were less predictable at an interannual scale, where mean annual temperatures ranged between 0.88 ± 0.12 (2017) to 1.29 ± 0.04 (2015) (**Fig. 4.2b**). Finally, lunar illumination followed highly predictable monthly cycles across all study years (**Fig. 4.2c**).

When compared to percent cover of sea-ice recorded in Scott Inlet throughout the study period, all shark detections coincided with the ice-free summer period and the arrival (in *undisturbed* years) and departure (both *disturbed* and *undisturbed* years) of tagged sharks occurred around the time of ice break-up and reformation, respectively (**Fig. 4.2a**). In contrast, records of temperature at approximate receiver depth did not display a predictable seasonal pattern across detection years, with no observed temporal trend relative to shark detections (**Fig. 4.2b**). Similarly, Greenland shark detections did not correspond to variation in lunar illumination, however, this comparison was complicated the resolution of the two datasets (*i.e.*, lunar data varying over monthly cycles compared to apparent seasonal variation in Greenland shark presence).

A correlation matrix of all non-categorical fixed effects (*i.e.,* excluding the biological variables *sex* and *age-class*) found strong negative relationships between the temporal variables, *ordinal date* and *month*, and the environmental variable, *ice cover* (**Fig. 4.3**). Weaker positive relationships were observed between these temporal variables and *temperature*, and to a lesser degree, *lunar illumination*. *Ice cover* and *temperature* also showed a weak negative correlation. Consequently, the two temporal variables *ordinal date* and *month* were excluded from the final model.

Results from the GLMM identified *percent ice cover* as a significant predictor of Greenland shark presence in the coastal fjord during the study period (**Table 4.2**). In contrast, the remaining fixed effects, including the biological variables, *sex* and *age class*, and the environmental variables, *temperature* and *lunar illumination*, were found not to be significant.

4.3.1.3 Detection span and frequency

Following tagging, Greenland sharks were detected over a median DS of 7 days (IQR = 4-20, range = 3-54, $n=65$; mean = 12.5 ± 11.9 d) and a median of 4 DD (IQR = 3-8, range = 2-13, $n=65$; mean = 5.2 ± 2.89 d) before exiting the fjord. No significant differences in DS or DD were detected when compared across tagging years or based on shark sex or size (L_T). However, when sharks were divided into length-based age-classes, DS was found to be greater for juveniles (median = 15, IQR = 5-24, range = 3-54, $n=17$; mean = 18 ± 14.63 d) than for subadult sharks (median = 5.5 d, IQR = 4-14, range = 3-49, $n=48$; mean = 10.52 ± 10.21 d) during the post-tagging, *disturbed* period (Wilcoxon rank sum coefficient = 552, $p<0.05$; **Fig. 4.4a**).

Of the 65 sharks tagged, 25% returned to the fjord following periods of absence ranging from 278 – 728 d (median = 332 d), with several sharks detected for up to three subsequent years after the year of release (14% detected over 2 y, 9% over 3 y, and 2% over 4 y) (**Fig. 4.5**). During these *undisturbed* events, sharks remained in the fjord for a median DS of 25 d (IQR = 2.75 - 66.25, range=1-99, $n=16$; mean = 27.7 ± 32.16 d). No significant differences in DS or DD were detected across entry or capture years (**Fig. 4.6**), however, DS and DD differed significantly based on L_T (Spearman's rank coefficient = 3545.7, $p<0.05$ and Spearman's rank coefficient = 3849.3, $p<0.05$, respectively). DS and DD were also differed between the two age-classes, with juveniles being detected significantly more often and over longer durations than subadults (DS Wilcoxon rank sum coefficient = 112, $p<0.05$; DD Wilcoxon rank sum coefficient = 116.5, $p<0.05$; **Fig. 4.4b**).

4.3.2 Use of deep-water channels

4.3.2.1 Locations of entry and exit

Greenland sharks demonstrated relatively consistent patterns of entry and exit location across years, with 76% of exit events (*n=89 events*) and 71% of re-entry events (*n=24*) recorded on the outermost gate G07 which spans perpendicularly across the deep-water channel connecting the study system with offshore Baffin Bay (**Fig. 4.7**). Exceptions included exit events detected on gates G03 (*n=1*), G05 (*n=5*), G06 (*n=2*), spanning channels in the inner fjord, southern basin, and Sam Ford fjord, respectively, and in the southern region of the grid array on gate G12 (*n=1;* **Fig. 4.1**).

The first of these instances highlighted the only mortality observed for all sharks tagged throughout the study period (shark ID: 101414). This shark was tagged on Sept. 30th, 2014 and was first detected by receivers in the inner fjord (G03 & G04) on Oct. 3rd and 4th prior to spending the following 46 days undetected, presumably moving through the unmonitored inner channels of the fjord. The shark was then redetected from Nov. 18th-20th by receivers in gate G03 where the last detection, recorded on Nov. 20th, 2014, demonstrated that the individual did not leave the study system and was therefore considered to be deceased.

The only exit event to be detected by a receiver belonging to the grid portion of the array was recorded on gate G12. This shark (shark ID: 101630) was tagged on Sept. 9th, 2016 in the inner fjord and was detected by a total of 29 receivers across 10 gates before the final detection was recorded 41 days later on gate G12.

For exits detected by gates G05 and G06, the locations of these gates indicated the use of deep-water channels to direct movements between coastal and offshore waters, similar to those for gate G07.

4.3.2.2 Influence of bottom depth on movements within deep-water channels

When the number of sharks detected was compared to the depth of stations within the primary receiver gates G01-G06 (**Fig. 4.1**), no consistent relationship between receiver location, depth, and the total number of sharks detected was observed (**Fig. 4.8**). However, for gate G07, located across the main channel between the fjord and offshore Baffin Bay and acting as the main entry/exit point for sharks, the number of detected individuals decreased with receiver depth (**Fig. 4.8a**). For this gate, the highest number of sharks were detected by receivers near the slopes bordering the deep-water channel at depths between ~400 and ~600 m. In contrast, receivers in gate G07 with the fewest detected individuals were located (i) in the centre of the channel at ~700 m depth and (ii) at the shallowest points at the end of the gate at bottom depths of <300 m (**Fig. 4.8a**).

4.3.3 Home ranges

Across all years for which the complete array was present (2014-2018), the estimated home range of Greenland sharks was located within the inner channels and at the mouth of Scott Inlet (**Fig. 4.9**). The core home range was localized to the region surrounding the innermost gates, G03 and G04, with secondary hotspots centered around primary gates at the mouth of the fjord (G01-G02), in the southern basin (G05) and at the northern end of gate G07 (**Fig. 4.9**).

Minor variation in the home range estimates of juvenile and subadult sharks was observed. For subadults, the home range estimated near the mouth of the fjord was centred around the southern channel near gate G02, and the southern hotspot near gate G05 was positioned away from the coastline (**Fig. 4.9b**). In contrast, the estimated home range of juvenile animals encompassed a larger portion of the northern channel mouth near gate G01 and extended out into the central basin along the northern channel bank (**Fig. 4.9a**). The home range of juvenile sharks also remained closer to shore in the southern basin near gate G05, with an additional hotspot in Sam Ford fjord (**Fig. 4.9a**). Both age-classes were found to use a similar proportion of the total available habitat, with juvenile and subadult 95% home ranges encompassing 22% and 24% of the array area, respectively (**Fig. 4.9**).

4.4 Discussion

In seasonal environments, such as Arctic coastal waters that are subject to extreme shifts in ice cover and productivity (Tremblay et al., 2012), animals must either adapt to recurring environmental shifts or undertake timed, long-distance movements that allow them periodic access to more suitable conditions. Many mobile, Arctic marine mammals demonstrate the latter, leading to highly transient life history strategies marked by frequent seasonal movements between coastal and offshore habitats (Dueck, Hiede-Jørgensen, Jensen, & Postma, 2007; Laidre et al., 2004; Marcoux, Ferguson, Roy, Bedard, & Simard, 2017). While the movement of marine mammals into productive coastal waters during the ice-free summer months is expected (due to their need for open water to breathe), it is less clear why a deep-water elasmobranch such as the Greenland shark would follow such a strict, ice-mediated regime. Nevertheless, this study demonstrates that the presence of tagged Greenland sharks in this model coastal fjord follows a highly predictable seasonal trend that mirrors seasonal fluctuations in sea-ice cover in the region across multiple years (**Fig. 4.2**). Furthermore, the importance of sea-ice as a predictor of Greenland shark presence was confirmed by the results of our GLMM (**Table 4.2**).

Previous research on other mobile Arctic species has demonstrated patterns in seasonal residency in Scott Inlet that closely resemble that of the Greenland shark. For example, the occurrence of narwhal (*Monodon Monoceros*) and bowhead whales (*Balaena mysticetus*) in the system correlates to the summer open water period, with movements between coastal and offshore waters triggered by ice break-up and reformation (Heide-Jørgensen, Dietz, et al., 2003; Heide-Jørgensen, Laidre, et al., 2003). Additional research on a deep-water species, the Greenland halibut (*Reinhardtius hippoglossoides*), revealed two overall patterns in coastal residency within Scott Inlet and Sam Ford fjord (Barkley et al., 2018). Similar to tagged Greenland sharks, the majority of acoustically-tagged Greenland halibut were detected in the coastal region in the late summer months and were observed exiting the fjord around the time of ice formation in November and December (Barkley et al., 2018). However, in contrast to our study, a subset of the tagged Greenland halibut population were classified as temporary residents, with individuals returning to the fjord during the winter months (under ice) and remaining there throughout most of the year (Barkley et al., 2018).

Given the importance of Greenland halibut in the diet of Greenland sharks (Leclerc et al., 2012), the concurrent presence of these two species in Scott Inlet could indicate that the observed seasonality of Greenland shark residency is influenced by the availability of Greenland halibut. However, the absence of Greenland halibut in the inner channels of the fjord (N.E. Hussey, pers. comm.), combined with the frequent occupation of these regions by tagged Greenland sharks, suggests that further studies comparing the core areas used by each species are required to confirm the nature of this relationship.

The degree of similarity between the movement patterns of this commercially exploited species (*i.e.*, Greenland halibut) and the Greenland shark (a primary bycatch species in Greenland halibut fisheries) also has important implications for fisheries management. While neither Greenland halibut nor Greenland sharks are currently targeted in inshore waters during the summer months, a shared shift in distribution to winter offshore habitats would suggest that fisheries targeting Greenland halibut in the offshore at that time of the year are also likely to encounter Greenland sharks. Importantly, while some Greenland halibut remain resident in coastal fjords throughout the winter, supporting the development of community ice-based fisheries (Barkley et al., 2018), our study also suggests that Greenland sharks would be exempt from this fishing pressure due to their absence from the system during the ice-covered months. However, despite our lack of winter detections, reports of sharks captured in the fjord on experimental longlines do exist (Walsh, 2018). This may suggest that, despite our sample size and monitoring duration, additional behavioural variation is present in the sampled shark population and requires further investigation.

Patterns of temporary coastal residency similar to that of the Greenland shark have also been demonstrated by mobile shark species that inhabit lower-latitude regions. For example, movement data from juvenile Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) tagged in Florida demonstrated that periods of coastal residency lasted between 1-35 d, and upon exiting the system, tagged sharks returned after a maximum period of absence of 1,352 d (Carlson et al., 2008). These findings highly resemble those of tagged Greenland sharks that remained in coastal waters for a median 25 d (in *undisturbed* years) and demonstrated a maximum length of individual absence prior to return of 788 d (shark ID: 101544, **Fig. 4.5**).

Furthermore, size-based differences in the importance of coastal systems are common among sharks, as coastal habitats often serve as refuges for neonates and juveniles due to high frequencies of intraspecific predation (Guttridge et al., 2012). In the current study, juvenile Greenland sharks showed extended periods of detection in both tagging and return years and were detected more frequently upon returning to the fjord relative to subadult sharks (**Fig. 4.4**). This residency behaviour also corroborates the findings of Hussey et al. (2015), wherein the Scott Inlet/Sam Ford fjord system was proposed as an important habitat for juvenile sharks following frequent captures of animals in this age-class on longlines in the region over a 3-year period (relative to other sites across the Canadian Arctic). However, despite differences in the duration of coastal residency exhibited by juvenile and subadult Greenland sharks (**Fig. 4.4**), the spatial extent of core use areas were highly similar between the two age-classes, with a preference for the inner channels of the fjord (gates G03 & G04) and just under ¼ of the array area encompassed by the 95% home ranges of each group (22% for juveniles, 24% for subadults) (**Fig. 4.9**). This lack of spatial segregation among individuals varying in size, as well as the prevalence of capture-associated cannibalism among Greenland sharks (Nielsen, Hedeholm, Simon, & Steffensen, 2014), suggests that intraspecific predation is likely to occur in Scott Inlet. Given little information on the occurrence of juvenile

Greenland sharks, these combined data highlight the importance of this region for this life stage, further supporting its designation as a conservation area with regulated fishing (Hussey, Cosandey-Godin, et al., 2015).

One unique benefit of our multi-year tracking dataset was that it allowed us to compare the movement behaviours exhibited by sharks immediately following tagging to those displayed by the same individuals in subsequent years upon returning to the system. Despite the relatively low return rates recorded (25% of individuals returned at least once), these *undisturbed* detection events revealed that animals enter coastal waters much earlier in the season than the time during which animals are typically tagged (September). This suggests that the typical timing of Greenland shark tagging in Scott Inlet greatly limits the potential duration of post-tagging detection and excludes a large portion of the typical period of seasonal residency exhibited by this species. As a result, sharks returning to the fjord were detected much earlier (first detected in late July as opposed to late September) and remained in the array for much longer durations (median 25 d, range=1-99, *n=16*) than was observed during *disturbed* detection periods (**Fig. 4.7**). Notably, similar durations of post-tagging residency were observed for Greenland sharks tagged with mrPATs and miniPATs near Grise Fiord in the late summer of 2015 (Hussey et al., 2018). In the latter case, two tagged individuals remained resident in the region for 5 and 10 d following tagging before undertaking large-scale movements to northwestern Greenland where, overall, tagged sharks then spent an average of 15 d in coastal waters (range=10-22, *n=5*; Hussey et al., 2018). Similarities between the timing of shark tagging conducted by Hussey et al. (2018) and that of the current study, support the theory that the duration of post-tagging coastal residency may be limited by late-summer tagging efforts that precede the seasonal transition of Greenland sharks away from coastal environments. This has implications for the application of short-term acoustic telemetry studies to examine residency behaviours and habitat use in mobile species.

An alternative theory is that behavioural modifications resulting from stress incurred during the process of capture, tagging, and release may have influenced the duration of post-tagging residency periods reported by both the current, and previous tagging studies. Capture-induced stress is of particular concern for deep-water species (such as the Greenland shark) that must be brought to the surface for tagging and, as a consequence, are likely to experience acute changes in ambient temperature and pressure (Edwards et al., 2019). Post-release behavioural modifications have also previously been documented in a number of tagged species including sea birds (Phillips, Xavier, & Croxall, 2003), pelagic teleosts (Abascal, Mejuto, Quintans, & Ramos-Cartelle, 2010; Hoolihan, 2005), and sharks (Campana et al., 2009; Hoolihan et al., 2011; Nakano, Matsunaga, Okamoto, & Okazaki, 2003), resulting in concern over the reliability of tagging records in providing accurate representations of naturally-occurring animal behaviours. Examination of the post-release behaviour of Greenland sharks has shown that vertical movement patterns are altered in the short time-frame immediately following tagging and release, but that sharks return to normal vertical movements and swim speeds after ~12 h (Watanabe et al. unpublished). Moreover, while sharks in this study demonstrated much longer seasonal residency in return *vs.* post-tagging detection periods, the median date of exit from the fjord was similar between the two, with sharks leaving the fjord approximately 4 days earlier in re-entry years. This suggests that while fine-scale behaviours may be altered immediately follwing tagging, there was no major effect on the duration of coastal residency exhibited by tagged Greenland sharks. Future research on the movement ecology of Greenland sharks could provide insight into post-tagging modification of horizontal movements displayed by this species.

Upon examining the locations of shark entry and exit from the study system, the majority of tagged Greenland sharks were found to use the main deep-water channel as a corridor to direct movements between the coastal system and offshore waters (**Fig. 4.7**). Furthermore, sharks appeared to use channel slopes at depths >300 m, along the shallower banks of the fjord's deep-water channels, as opposed to transiting through the deepest waters at the channel's centre (**Fig. 4.8**). This may indicate the use of bathymetric characteristics such as slopes to guide the movements of this visually impaired species throughout coastal deep-water systems.

Broad-scale depth-oriented movement (based on catch records) has been documented in a number of deep-sea fishes and decapod crustaceans, where, similar to the Greenland shark, seasonal migrations were directed between deeper habitats occupied during the winter and shallower regions occupied throughout the spring and summer (Aguzzi et al., 2013). In contrast, little is known about the navigational cues used by deep-water species to orient movements through environmental landscapes at a finer spatial scale. This is likely due to the current lack of telemetry technologies rated for use in deep-water that provide both fine-scale movement data and simultaneous records of environmental conditions (*e.g.,* depth and temperature) (Edwards et al., 2019). Of the limited fine-scale movement records available for deep-water species, very few report the identification of navigational cues. One example, a highly localized study (500 m radius) on the movements of abyssal grenadiers at >4,000 m depth, found that fish used current direction as a cue to orient movements toward the source of odour plumes (Bagley, 1993). An additional study that reported on the fine-scale movements of Cuban dogfish (*Squalus cubensis*), a deep-water elasmobranch, suggested that vertical movement in this species may be influenced by a preference for certain bathymetric features (Shipley, Howey, Tolentino, Jordan, & Brooks, 2017). Further evidence of navigation based on bathymetric cues was demonstrated by sea lamprey that used depth-based orientation to direct movements toward coastlines in shallow waters (21-39 m depth) (Meckley, Gurarie, Miller, & Michaelwagner, 2017). To facilitate the further study of fine-scale movement and spatial orientation in deep-water species, technological innovations are needed to facilitate the collection of movement data at improved spatial resolutions, in addition to simultaneous records of archived environmental data.

Scott Inlet is the proposed site of a community-based Greenland halibut fishery that is currently under development with support provided by the Department of Fisheries and Oceans Canada (DFO) (Walsh, 2018). Furthermore, predicted reductions in sea ice cover and higher Arctic temperatures will undoubtedly lead to increased fishing pressure across all polar marine regions in the coming years (Christiansen, Mecklenburg, & Karamushko, 2014), including the expansion of community fisheries to target Greenland halibut in the summer *vs.* the winter (Hussey et al., 2017). As Greenland sharks become increasingly vulnerable to incidental capture throughout their known range, an understanding of the seasonal distribution and movement behaviours of this species is essential to ensure that appropriate management efforts are put in place. This study provides critical insights into the timing of Greenland shark presence in Scott Inlet, a model coastal Arctic fjord.

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TABLES/FIGURES

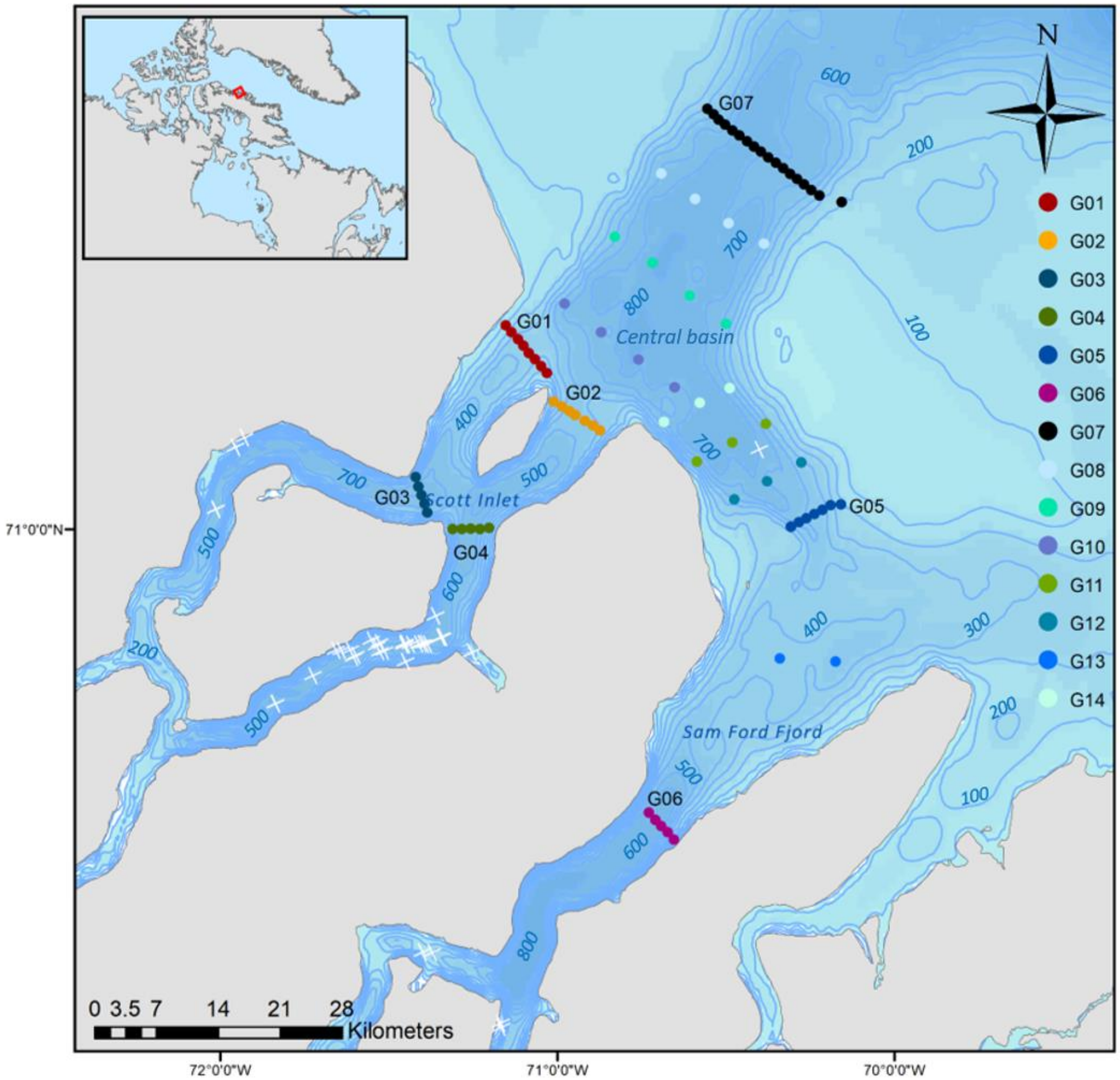

Fig 4.1 | Locations of moored acoustic receivers (filled circles) and the release locations of tagged Greenland sharks (X) in the Scott Inlet/Sam Ford Fjord acoustic array (ASI), located on eastern Baffin Island, Nunavut (Eastern Canadian Arctic). Primary receiver gates spanning deep-water channels are labelled (G01-G07), while secondary receiver gates (G08-G14) form the central grid. Blue contour lines represent 100 m depth isobaths.

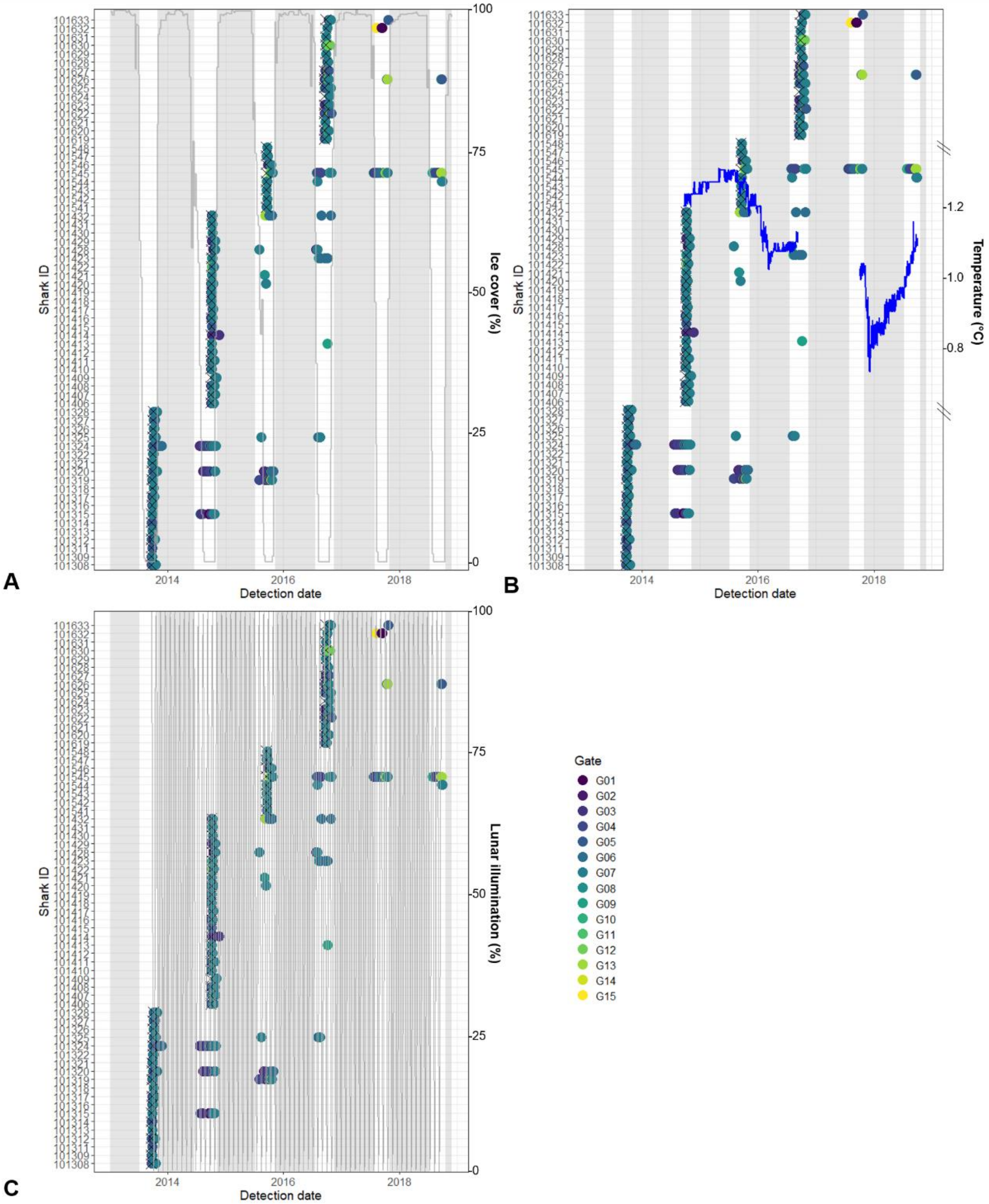

Figure 4.2 | Detection profiles of Greenland sharks (*S. microcephalus*) tagged with acoustic transmitters between 2013 and 2016 in Scott Inlet (Nunavut), plotted against environmental records for A) weekly percent sea-ice cover, B) daily temperature (ºC) at approximate receiver depth (~789 m), and C) daily percent lunar illumination. Detections are colour-coded by the receiver gate on which the animal was detected, and the date of tagging and release is denoted by an ‘X’. Shaded bars denote the annual periods of ice cover between the timing of formation (>75% sustained cover) and breakup (>75% sustained cover) throughout the study period.

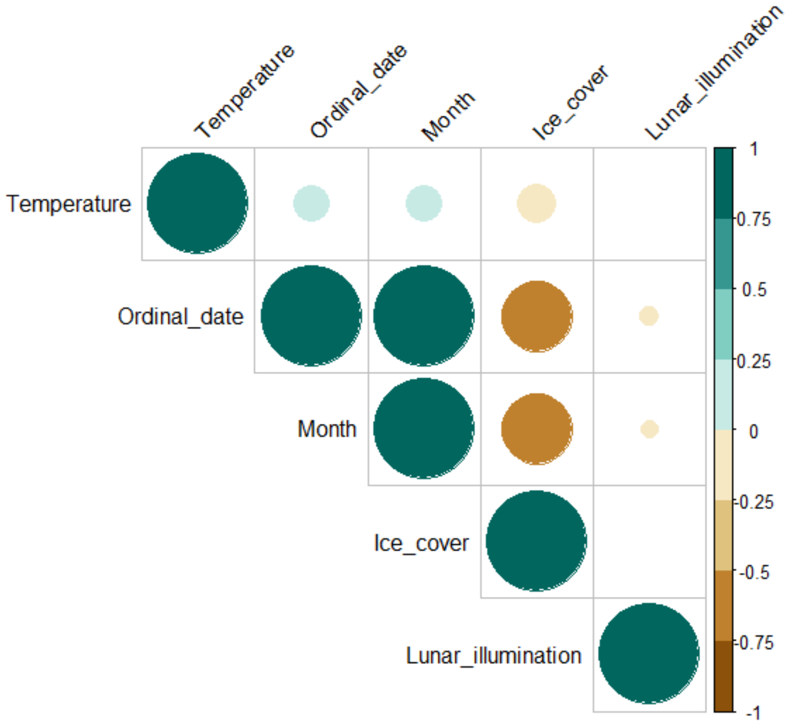

Fig 4.3 | Correlation matrix of continuous temporal (*Ordinal date* and *Month*) and environmental (*Temperature, Ice cover,* and *Lunar illumination*) variables recorded in the ASI acoustic array (Scott Inlet, Nunavut) between Sept 13th, 2013 and Sept. 27th, 2018.

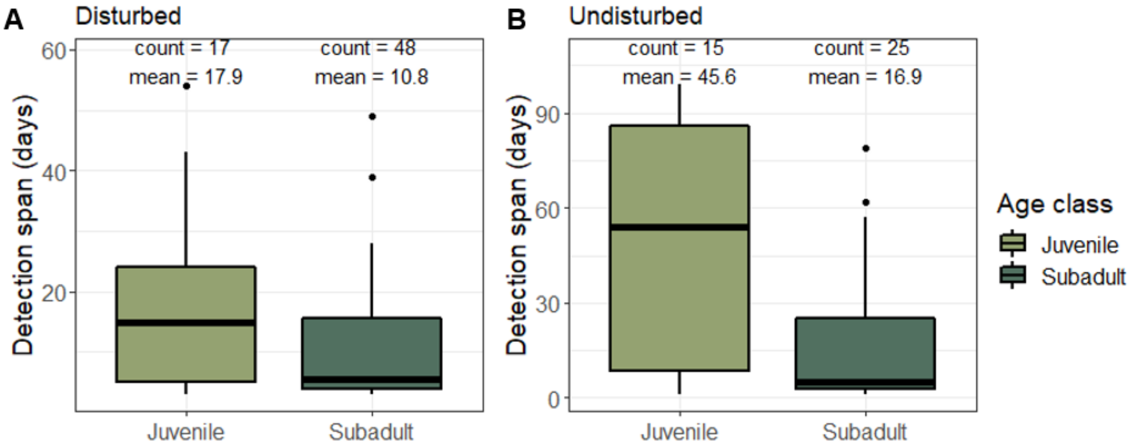

Figure 4.4 | Detection spans of Greenland sharks tagged between 2013 and 2016 in Scott Inlet (Nunavut), where detection span refers to the number of days a tagged shark is considered resident in the acoustic array system prior to a period of absence >60 days. Detection spans are grouped by age-class for juvenile (<200 cm L_T) and subadult (≤200 cm L_T) sharks during (A) post-release (*disturbed*) and (B) natural re-entry (*undisturbed*) detection periods.

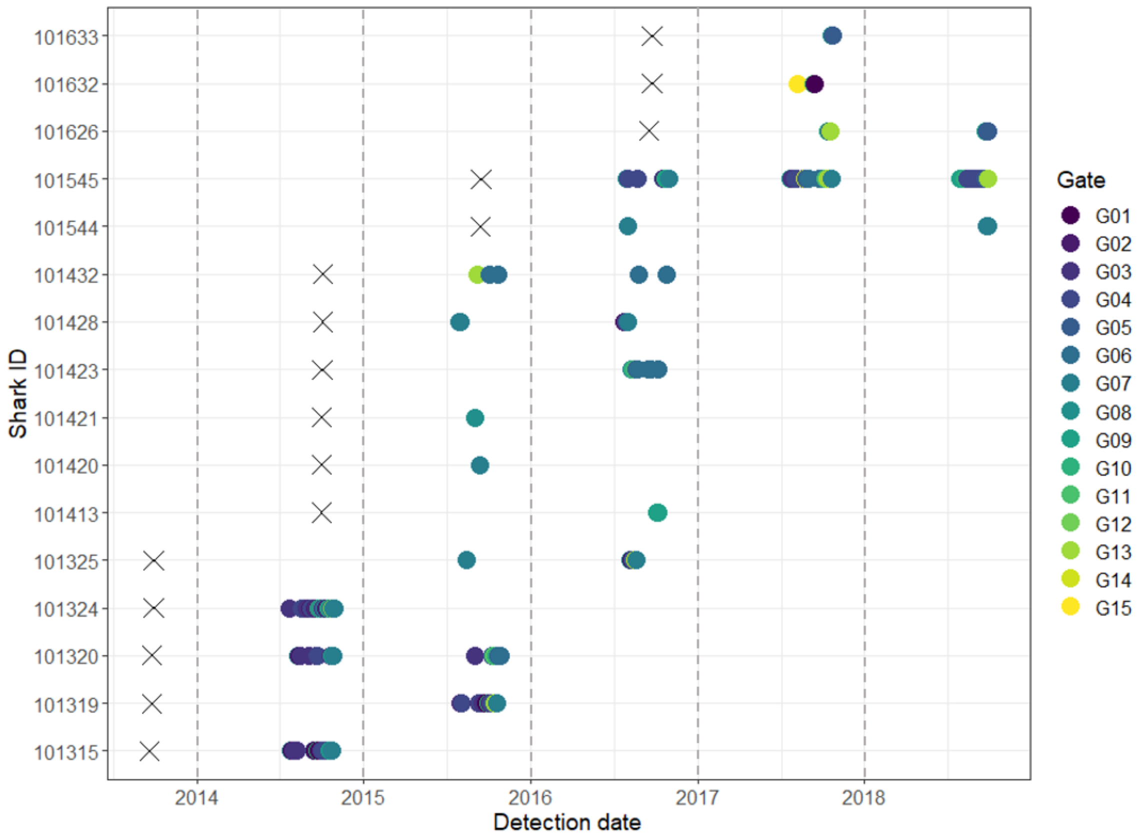

Figure 4.5 | Detection profiles of the re-entry (*i.e.*, *undisturbed*) events of Greenland sharks tagged between 2013 and 2016 in Scott Inlet, Nunavut (n = *16*). Detections are colour-coded by the receiver gate by which the shark was detected, and the date of tagging and release is denoted by an 'X'.

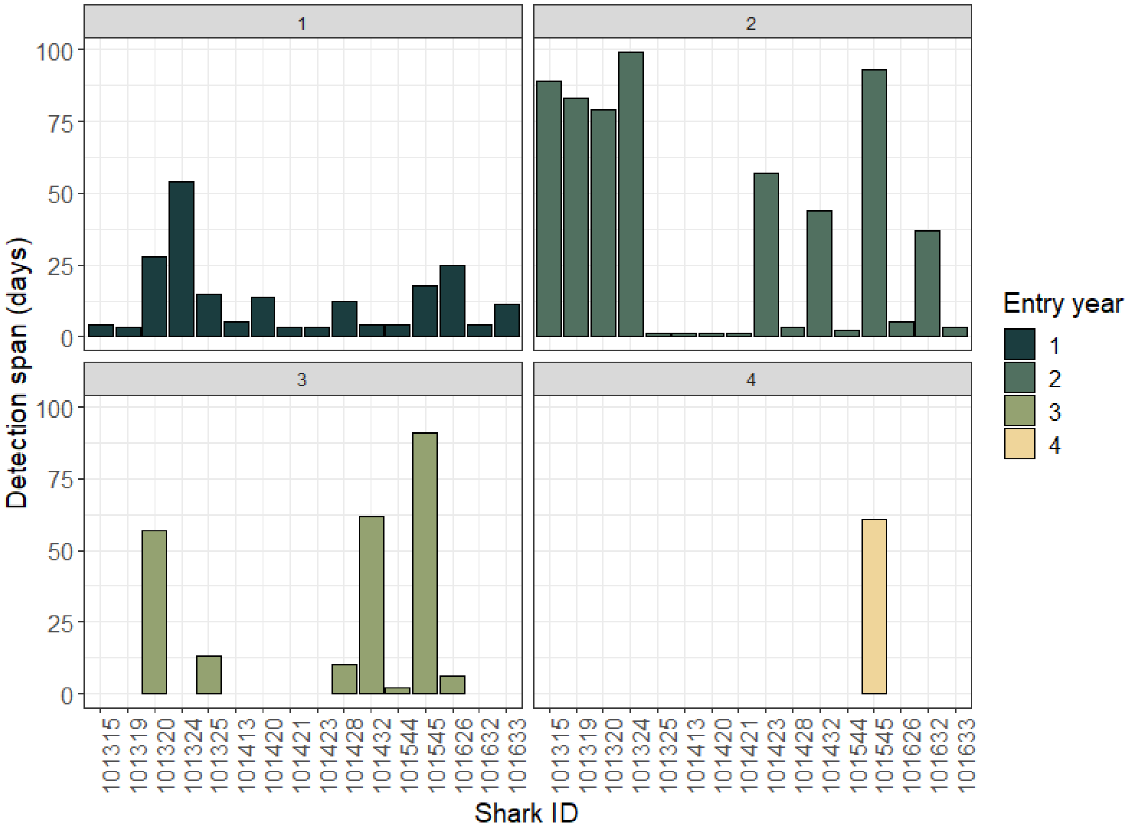

Figure 4.6 | Detection spans (DS) of Greenland sharks (*S. microcephalus*) tagged between 2013 and 2016 in Scott Inlet, Nunavut. Entry year denotes the number of subsequent years during which an animal was detected by the array, where entry year 1 represents the tagging year.

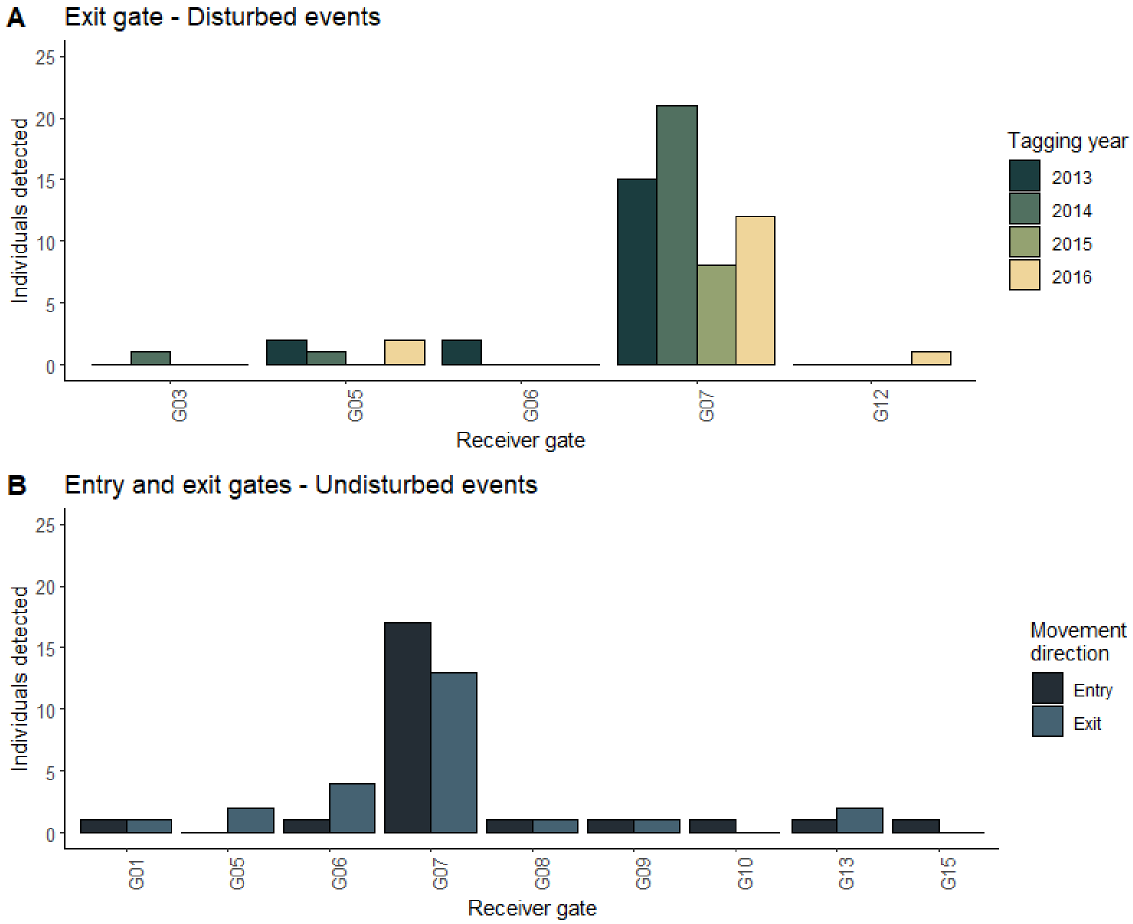

Figure 4.7 | Greenland shark entry and exit events detected on receiver gates in the Scott Inlet array (ASI), grouped by tagging year for post-tagging (*disturbed*) detections (A) and by movement direction (entry/exit) for natural re-entry (*undisturbed*) events (B).

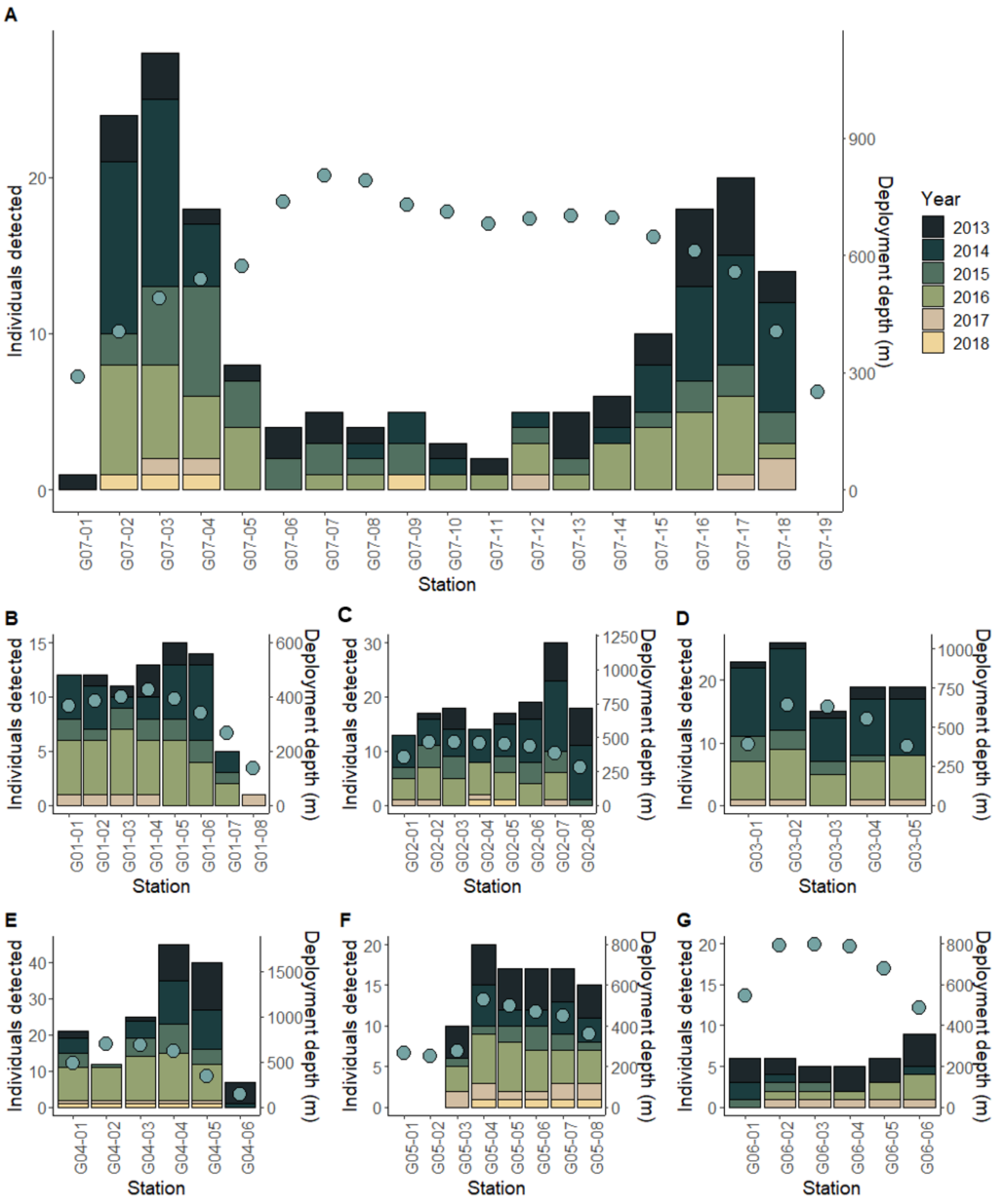

Figure 4.8 | Detection rates of individual tagged Greenland sharks grouped by receiver station (as a proxy for depth) and detection year in the ASI array. Panels depict receiver stations arranged by gate: A) G07, B-G) G01-G06. Deployment depth for each station is depicted as the mean bottom depth at the deployment location, calculated across each station’s active deployment period.

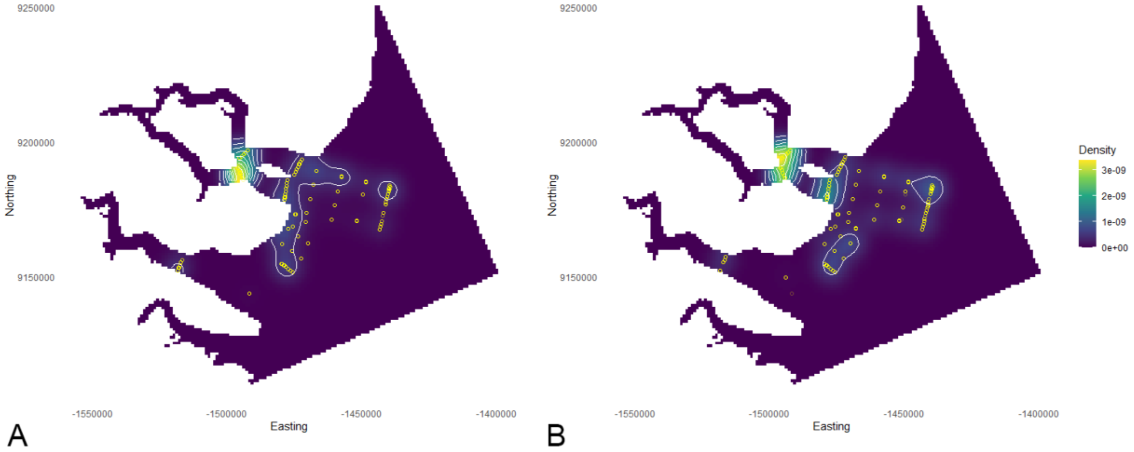

Figure 4.9 | Lattice-based estimations of the 95% home ranges of (A) juvenile (<2 m L_T; *n* = *17*) and (B) subadult (≥2 m L_T; *n* = *48*) Greenland sharks detected in the ASI array (Scott Inlet, Nunavut) between 2014 and 2016.

Table 4.1 | Summary of post-release residency for Greenland sharks tagged in Scott Inlet, Nunavut between 2013 and 2016 and detected on receiver gates G01-G07 of the ASI array. Detection delay is reported as the number of days between the release date and the date the animal was first detected on a receiver within the array. Residency metrics include: the number of days during which an animal was detected (detection days) and the number of days between the animal's first and last detections before a prolonged period of absence (>60 d; detection span). Also included are the total number of receivers that detected and individual, as well as the total number of years over which these detections occurred.

Shark ID	Sex	Total length (m)	Age-class	Release date	Detection delay (days)	Detection span (days)	Detection days	Total stations	Years detected
101327	M	2.57	Subadult	2013-09-29	2	11	3	5	1
101328	M	1.46	Juvenile	2013-09-29	5	19	4	6	1
101308	F	1.94	Juvenile	2013-09-18	3	25	9	15	1
101309	F	2.85	Subadult	2013-09-18	3	3	2	6	1
101311	M	2.95	Subadult	2013-09-18	5	3	3	5	1
101312	F	2.89	Subadult	2013-09-18	2	21	10	20	1
101316	F	3.12	Subadult	2013-09-24	1	5	3	5	1
101317	F	1.5	Juvenile	2013-09-24	2	13	5	5	1
101318	F	1.57	Juvenile	2013-09-24	8	4	3	6	1
101319	M	1.72	Juvenile	2013-09-24	2	3	3	6	2
101320	F	2.67	Subadult	2013-09-24	4	28	13	15	3
101321	F	2.5	Subadult	2013-09-24	2	4	3	6	1
101322	M	2.85	Subadult	2013-09-27	2	6	4	5	1
101324	F	1.89	Juvenile	2013-09-28	2	54	13	12	2
101325	F	1.86	Juvenile	2013-09-28	4	15	4	7	3
101313	M	2.16	Subadult	2013-09-18	5	4	3	8	1
101314	M	2.8	Subadult	2013-09-19	3	3	3	5	1
101315	M	1.81	Juvenile	2013-09-19	4	4	3	6	2
101326	F	2.75	Subadult	2013-09-29	4	7	3	7	1
101432	M	2.82	Subadult	2014-10-02	3	4	4	5	3
101406	M	2.36	Subadult	2014-09-27	4	20	11	20	1
101407	M	2.20	Subadult	2014-09-27	6	23	8	16	1
101408	F	2.80	Subadult	2014-09-27	5	21	8	14	1
101409	F	2.43	Subadult	2014-09-30	28	8	4	11	1
101410	M	2.92	Subadult	2014-09-30	1	4	3	8	1
101411	M	2.94	Subadult	2014-09-30	3	20	9	20	1
101412	F	3.41	Subadult	2014-09-30	5	6	3	9	1
101413	F	3.23	Subadult	2014-09-30	3	5	3	8	2
101414	M	2.79	Subadult	2014-09-30	3	49	5	4	1
101415	M	2.65	Subadult	2014-10-01	2	4	3	8	1
101416	M	2.80	Subadult	2014-10-01	1	7	5	10	1
101417	M	2.47	Subadult	2014-10-01	10	3	3	4	1

101418	M	2.71	Subadult	2014-10-01	1	4	3	13	1
101422	M	2.86	Subadult	2014-10-02	2	13	6	20	1
101423	F	1.93	Juvenile	2014-10-02	3	4	3	8	2
101428	M	2.34	Subadult	2014-10-02	12	12	6	8	3
101429	M	2.21	Subadult	2014-10-02	3	23	10	9	1
101430	M	2.70	Subadult	2014-10-02	6	3	3	9	1
101431	F	2.54	Subadult	2014-10-02	2	4	3	7	1
101419	M	2.72	Subadult	2014-10-01	1	4	3	7	1
101420	F	2.84	Subadult	2014-10-01	1	14	8	14	2
101421	M	2.98	Subadult	2014-10-01	3	3	3	7	2
101547	F	3.30	Subadult	2015-09-13	3	8	3	10	1
101548	M	3.00	Subadult	2015-09-14	5	3	3	5	1
101541	M	2.20	Subadult	2015-09-12	3	7	4	13	1
101542	F	2.78	Subadult	2015-09-13	5	4	3	7	1
101543	F	3.00	Subadult	2015-09-13	2	3	3	7	1
101544	M	2.22	Subadult	2015-09-13	3	4	3	8	3
101545	M	1.82	Juvenile	2015-09-14	23	18	5	19	4
101546	M	1.78	Juvenile	2015-09-14	9	24	8	19	1
101627	M	2.86	Subadult	2016-09-16	3	22	8	16	1
101628	M	1.63	Juvenile	2016-09-22	11	6	3	7	1
101630	F	2.80	Subadult	2016-09-22	1	15	8	29	1
101629	F	2.90	Subadult	2016-09-22	1	4	3	13	1
101626	M	2.70	Subadult	2016-09-16	1	25	8	27	3
101622	F	1.82	Juvenile	2016-09-15	1	43	6	13	1
101619	M	1.88	Juvenile	2016-09-14	3	13	8	17	1
101620	M	1.97	Juvenile	2016-09-14	4	24	8	20	1
101621	M	2.21	Subadult	2016-09-14	6	3	3	8	1
101625	M	3.12	Subadult	2016-09-16	1	39	12	21	1
101623	M	1.92	Juvenile	2016-09-15	1	32	9	20	1
101624	M	1.92	Juvenile	2016-09-15	29	5	3	7	1
101631	M	2.23	Subadult	2016-09-22	1	4	3	9	1
101632	M	2.78	Subadult	2016-09-22	10	4	4	9	2
101633	M	2.53	Subadult	2016-09-22	21	11	6	13	2

Table 4.2 Results of the generalized linear mixed effects model performed on five years of Greenland shark presence/absence data from the ASI acoustic array in Scott Inlet, Nunavut.

Random effect	**Variance**	***SE***		
Shark ID	0.17	0.23		
Fixed effects	**Value estimate**	***SE***	**t-value**	**p-value**
Intercept	0.44	0.11	3.89	0.00
Sex (M/F)	0.04	0.07	0.58	0.57
Age class (Sub/Juv)	-0.06	0.08	-0.74	0.47
Ice cover (%)	0.00	0.00	-12.37	**0.00**
Temperature (°C)	-0.05	0.06	-0.75	0.45
Lunar illumination (%)	0.00	0.00	0.88	0.38

CHAPTER 5

Multi-year acoustic tracking reveals transience and apparent seasonality in the coastal-offshore movements of Greenland sharks (*Somniosus microcephalus*)

5.1 Introduction

Resource distribution plays a key role in regulating the movements of consumers across environmental landscapes (O'Neill, Milne, Turner, & Gardner, 1988). In seasonal environments, the occurrence of resource patches (primary productivity hotspots and prey aggregations) can vary substantially across time and space, producing patterns which are often reflected in the movements of mobile consumers (Boyd, Staniland, & Martin, 2002; Laidre et al., 2004; Sims, Southall, Richardson, Reid, & Metcalfe, 2003). As a result, mobile consumers drive food web stability by coupling parallel energy pathways from disparate sources of primary productivity (McCann, Rasmussen, & Umbanhowar, 2005; McMeans et al., 2013; Williams, Papastamatiou, Caselle, Bradley, & Jacoby, 2018), and by adopting a flexible response to changing resource conditions that maximizes energy flow (McCann et al., 2005). For example, Arctic marine environments are characterized by extreme seasonality in solar radiation and the extent of sea-ice cover which determine both spatial and temporal variability in pelagic and ice-associated primary production and in turn, the distribution of resource hotspots (Gradinger, 1995; Tremblay et al., 2012). In Baffin Bay, a deep-water ocean basin situated between the Eastern Canadian Arctic and West Greenland, this seasonal variability has been shown to influence the movements of marine predators, leading to patterns which predominantly coincide with the timing and location of sea-ice formation and retreat [*e.g., Monodon Monoceros* (Laidre et al., 2004), *Balaena mysticetus* (Dueck, Hiede-Jørgensen, Jensen, & Postma, 2007), *Odobenus rosmarus*, *Erignathus barbatus*, (Marcoux, Ferguson, Roy, Bedard, & Simard, 2017) and

Reinhardtius hippoglossoides (Barkley, Hussey, Fisk, Hedges, & Treble, 2018; Hussey et al., 2017)]. Specifically, the presence of transient marine animals in the deep-water fjords of Baffin Island [*e.g.*, *R. hippoglossoides*, (Barkley et al., 2018), *M. Monoceros*, and *B. mysticetus*, (Marcoux et al., 2017)] corresponds tightly with the summer open water period when increased upwelling and nutrient inputs from glacial and terrestrial runoff stimulate primary productivity in these coastal systems (Gradinger, 1995; Tremblay et al., 2012). Conversely, in the ice-covered winter months, offshore areas of significant upwelling and reduced ice cover such as the North Water (NOW) Polynya act as hotspots of late-season primary productivity that promote the aggregation of numerous marine mammals and birds (Heide-jørgensen et al., 2013; Melling et al., 2001). In this seasonally dynamic environment, a high degree of mobility and the predictable spatial and temporal occurrence of primary productivity allows large-bodied consumers to exploit these brief and intermittent resource patches despite the landscape's vast spatial scale.

In addition to spatial and temporal segregation of resources, consumer mobility is also influenced by the degree to which resources are available within an ecosystem. For instance, under sparse resource conditions, animals are required to operate at broader scales of habitat utilization in order to locate a larger number of resource patches (O'Neill et al., 1988). Deep-sea habitats are highly nutrient-limited, leading to the evolution of highly efficient resource detection traits (*e.g.*, chemoreception) and long-range mobility (Armstrong, Foley, Tinch, & van den Hove, 2012; Premke, Muyakshin, Klages, & Wegner, 2003). Depending on the scale of habitat use, high levels of mobility can drive migratory marine species to move through waters managed by numerous jurisdictions and, in turn, to encounter various levels of protection throughout their individual lifespans (Barkley et al., 2019; Heupel et al., 2015; Lascelles et al., 2014). The movement of wide-ranging species through regions varying in levels of both threats and protection can complicate conservation and management efforts (Heupel et al., 2015). Importantly, migratory marine species often include large-bodied predators that play disproportionately important roles in ecosystem stability (McCann et al., 2005) and may act as indicators of ecosystem health (Zacharias & Roff, 2001).

As the largest fish species to inhabit the Arctic deep sea, the Greenland shark (*Somniosus microcephalus*) occupies a high trophic position (4.8) as both scavenger and active predator and likely plays a key role in providing stability to Arctic marine ecosystems (Hussey et al., 2014; McMeans et al., 2013). While exhibiting the slowest observed mean swim speed (0.34 ms^{-1}) and tailbeat frequency (0.15 Hz) relative to body size for any fish species (Watanabe, Lydersen, Fisk, & Kovacs, 2012), Greenland sharks are capable of undertaking extensive horizontal movements (Campana, Fisk, & Peter Klimley, 2015a; Hussey et al., 2018) and maintain a broad distribution throughout the coastal and offshore waters of Baffin Bay (MacNeil et al., 2012). As such, this species is vulnerable to incidental capture year-round by both coastal community-based and offshore commercial fisheries that operate throughout their range in the Eastern Canadian Arctic (Bryk, Hedges, & Treble, 2018; Davis et al., 2013). Given their current designation as the world’s longest-lived vertebrate (Nielsen et al., 2016), and the fact that they possess other *K*-selected life history traits such as low fecundity, slow growth (0.5 cm yr^{-1}; Hansen, 1963), and extremely slow metabolic rates (Ste Marie et al. unpublished), the management of this species is of growing concern (Davis et al., 2013; Edwards et al., 2019).

Understanding whether mobile species exhibit relatively transient movement behaviours and/or philopatry, as well as a knowledge of how seasonality shapes species distributions, are critical components of risk assessments relating to the health of wild populations and the development of appropriate management strategies. Despite the predicted high abundance of Greenland sharks throughout the Baffin Bay region (Devine, Wheeland, & Fisher, 2018) and their vulnerability to incidental capture by commercial and Inuit community fisheries (Bryk et al., 2018; Idrobo & Berkes, 2012), Greenland shark distribution and the timing of movements throughout the basin remain unknown. The overall goal of the current study was therefore to examine the structure of Greenland shark movements in coastal and offshore waters in terms of: (i) determining repeat detections of sharks at receiver arrays across years as a measure of philopatry and quantifying detection events as a proxy for transient movements, (ii) identifying hotspots of occurrence (relative to spatial monitoring), and (iii) defining whether the species exhibits predictable spatiotemporal patterns of distribution between the two environments.

To achieve this, we examined the detection profiles of Greenland sharks recorded via static acoustic receivers deployed along the deep-water offshore banks of Baffin Bay (~3 y of monitoring, total area = ~34,458 km^2) and in 4 coastal environments (~7 y of monitoring, total area range = ~348 - 2,152 km^2). We hypothesized that the Greenland shark's long lifespan, high degree of mobility, and opportunistic foraging strategy would drive the species to adopt a temporally fluctuating distribution corresponding to the seasonal occurrence of resource patches throughout the basin and mirroring those reported for several Arctic predators. Specifically, we expected sharks to concentrate in coastal fjords during periods of peak coastal productivity (spring and summer), in contrast to the less productive winter months, when sharks would be dispersed throughout the ice-covered ocean basin.

5.2 Methods

5.2.1 Study site

Baffin Bay is a large, semi-enclosed ocean basin situated between Baffin Island (Nunavut, Canada) and Northwestern Greenland with a maximum depth of approximately 2000 m (**Fig. 5.1**). To the south, the bay is linked to the North Atlantic by a deep-water sill (640 m) in the Davis Strait, and in the north it connects to the Arctic Ocean via shallower sills located in Lancaster Sound (125 m depth), Jones Sound (190 m depth), and Nares Strait (220 m depth) (Münchow, Falkner, & Melling, 2015). Along its continental margins, Baffin Bay is ringed by wide, sloping shelf areas off Greenland, and more steeply sloping shelves off Baffin Island, both of which are broken by a series of deep channels (~500 – 1000 m depth) connecting offshore waters to its coastal fjords (Münchow et al., 2015). Circulation patterns in Baffin Bay are driven by two major North Atlantic current systems known as the West Greenland and Baffin Island Currents. Warm and salty water ($T > 0^{\circ}C$, $S > 34$) from the North Atlantic enters the bay from the south through the eastern Davis Strait, moving northward along the west coast of Greenland, where it is met by inflows of Arctic water from the Smith, Lancaster, and Jones Sounds (Tang et al., 2004). Following this cyclonic flow, the Baffin Island Current then moves southward down the eastern coast of Baffin Island, resulting in a prominent outflow through western Davis Strait (Tang et al., 2004). This deep-water basin is also characterized by seasonal, semi-complete coverage of sea-ice, with formation beginning in October, increasing in a southerly direction and reaching near-complete coverage in March (Tang et al., 2004). Predominantly ice-free periods occur only in August and September (Tang et al., 2004), however, a recurrent patch of open water known as the North Water (NOW) Polynya can typically found be spanning the region between Smith and Lancaster Sounds (~76˚N to 79˚N and 70˚W to 80˚W) throughout the ice-covered months (Heide-jørgensen et al., 2013).

5.2.2 Shark capture and tagging

Greenland sharks were tagged during the summer/fall field season (July-Oct) from 2012 to 2018 at 7 inshore sites along the Eastern coast of Baffin Island (see **Table 5.1**). Sharks were captured using bottom longlines (100-1500 m in length) set at depths between 400 and 1000 m for periods ranging from 3-12 h. Longlines were set with size 16, 18, and 20 circle hooks attached to 50 x 1.5 m steel leader gangions spaced 10 m apart and baited with either frozen squid, char, narwhal, or seal meat. Acoustic tagging was conducted using the following methods. Upon capture, each shark was held alongside an inflatable zodiac using tail and body straps while a 69 kHz acoustic transmitter (V16-6x, V16-TP-4x; VEMCO) was surgically inserted through a small incision on the animal's ventral side (anterior to the pelvic fins and just off the midline). The incision was then closed using 3-4 interrupted sutures. Tagging procedures, including measurement (total length [L_T; cm]) and biological sampling were conducted within ~10 min, after which time the shark was released at the capture location and was monitored for normal swimming behaviour.

5.2.3 Acoustic arrays

The movements of tagged Greenland sharks were monitored throughout the coastal and offshore regions of Baffin Bay (Eastern Canadian Arctic) via static acoustic telemetry. Static receiver stations designed for the detection of tagged sharks were constructed using two nylon risers which were anchored to the seafloor by a 200 lb cast iron disc anchor and connected to an acoustic release mechanism (PORT MFE; EdgeTech, West Wareham, MA, USA) positioned approximately 10 m above the anchor. Receiver stations were suspended vertically in the water column by a subsurface float. The length of the upper riser (connecting the float and the release) was selected relative to the bottom depth at the deployment location, with longer risers (187 m) deployed at depths >800 m and shorter risers (12 m) on shallower deployments (<800 m depth). Acoustic receivers (VR2W; VEMCO Ltd., Halifax, Nova Scotia) were attached to the upper riser approximately 2 m below the float using zip ties and gangion line. Equipment retrieval was facilitated by the acoustic release mechanism which, upon receipt of an acoustic command signal, released from the anchor riser allowing the upper riser, along with its associated acoustic receiver and environmental sensor, to float to the surface where it was recovered. Station servicing and data collection were conducted annually from late September to early October, during which time stations were typically retrieved and subsequently redeployed in their original locations within a 24 h period. Across all study years, stations were deployed at bottom depths ranging from 397 to 1150 m with a mean deployment depth of 535 ± 312.47 m. Receiver stations referred to in this study formed the basis of 6 separate arrays deployed across 4 coastal systems and in offshore waters along the western continental margin of Baffin Bay (**Table 5.1**). The maximum detection range of acoustic receivers was estimated at ~802 m based on range tests previously conducted at comparable depths (~1000 m) and under similar environmental conditions in Cumberland Sound, Nunavut (Hussey et al., 2017, Appendix S1).

5.2.4 Data analysis

Greenland shark detections were summarized using the statistical software R v.3.5.3 (R Core team, 2019) and the packages, *tidyverse* (Wickham, 2019) and *glatos* (Holbrook et al., 2020). All maps were produced using ArcMAP (Esri Inc., 2019) and additional figures were produced using the R package, *ggplot2* (Wickham, 2016).

Summary statistics were compiled for Greenland shark acoustic telemetry detections recorded on all coastal and offshore arrays. Offshore stations were classified as those deployed along the continental slope across a depth gradient between 600 and 1100 m while inshore stations were classified as all those deployed on the continental shelf between the coast and the shelf margins. Coastal arrays were deployed in Cumberland Sound (ACS), Tremblay Sound (ATS), Scott Inlet (ASI), and Qikiqtarjuaq (QIK), while offshore arrays included receivers deployed in southeastern Baffin Bay (DST and ABO) and along the western continental shelf (ABO) (**Table 5.1**). Detections recorded across all sites were used to compare the relative number of tagged sharks present in each array, as well as annual returns to each location, the timing of Greenland shark movements, and the scales of connectivity exhibited by sharks transiting throughout the basin. Detection events recorded by offshore receivers were further examined as a proxy for transient movement behaviour.

5.2.3.1 Summarizing Greenland shark detections across all inshore and offshore receiver arrays

For each receiver array, the active deployment period and the number of receivers that formed each array were summarized over the 7-y study period (**Table 5.1**). The total number of detections recorded per array, the number of tagged individuals detected, and the proportion of receivers that detected the presence of tagged sharks were then calculated for the entire study period (**Table 5.1, Fig. 5.1**). We acknowledge that the number of sharks detected in coastal *vs.* offshore regions is inherently biased by the fact that all tagged sharks were captured and released in coastal waters.

5.2.3.2 Examining the offshore presence of Greenland sharks

To examine Greenland shark presence in offshore waters, acoustic telemetry detections from a subset of tagged individuals that were captured and tagged between July 2011 and August 2017 were examined. Detection summaries were categorized at three levels of organization: by receiver array (**Figs. 5.1, 5.3, 5.7**), by offshore receiver gate or station (*i.e.*, array subcomponents; **Figs. 5.4, 5.8**), and by tagged individual (**Figs. 5.2, 5.5, 5.6**). Given the extent of the combined offshore arrays, which provide limited spatial coverage relative to the scale of the open water environment, coupled with a comparatively low number of detections recorded per receiver (with high zero inflation), we present an overview of Greenland shark presence and movement patterns and do not include statistical approaches.

5.2.3.3 Duration and periodicity of 'detection events' as a proxy for offshore transient movements

To examine the movement behaviours exhibited by Greenland sharks in offshore waters, the number of detections predicted for a Greenland shark transiting by a receiver at a known swimming speed was used as a proxy for transient movement. This value was then compared to the observed number of sequential detections recorded for individual sharks by offshore receivers. The expected number of detections for a transiting shark - based on an individual moving in a linear path across the widest diameter of the receiver detection range - was calculated based on:

i) A receiver detection radius of 802 m at 60% detection efficiency – as reported by Hussey et al. (2017).

ii) An average swim speed of 0.34 ms^{-1} for Greenland sharks (Watanabe et al., 2012).

iii) A minimum nominal tag delay of 200 sec (for a V16TP-4x tag).

Detections of tagged individuals recorded by each offshore receiver were classified into detection events – defined as clusters of sequential detections of a unique tag (*i.e.*, tagged shark) at a single receiver station –using the 'detection_events' function in the *glatos* R package (Holbrook et al., 2020) with a time separation interval value of 7 days (604800 sec). The latter value determines the maximum duration used to delineate individual detection events and was chosen as a conservative estimate of the average duration of detection events. The average number of detections and event duration for all unique offshore receivers was then calculated and compared to predicted values for an animal transiting past a receiver.

5.2.3.4 Examining coastal-offshore seasonality

To examine temporal patterns in the spatial distribution of Greenland sharks across inshore *vs.* offshore environments, detections were first combined across all arrays and study years and were visualized by month and receiver latitude. This visualization method was then repeated using only the coastal array that is most connected with the offshore (QIK). This was done to provide a finer scale for the examination of spatiotemporal movement patterns and to highlight variability in the abundance of sharks detected across offshore receiver stations and in coastal waters.

5.2.3.5 Individual-level movements and relative efficiency of offshore arrays

A subset of sharks that were detected by both coastal and offshore receivers during the 3 y of offshore array deployments (*n=48*) was used to examine individual-level movements between the two environments and to assess the efficiency of offshore array design for detecting tagged animals. Time periods when sharks were absent from the coastal array in which they were tagged were identified (*i.e.*, periods bounded by temporary coastal residency events - categorized as all coastal detections recorded within a given study year). It was assumed that these coastal absences represent time periods when individuals were not detected by coastal arrays and were therefore considered to be present either in an unmonitored coastal system or in offshore waters. The rate of shark detection by offshore arrays provides a measure of the efficiency of offshore receivers to detect tagged individuals. Absence periods for tagged sharks from coastal arrays were only considered if they occurred after the first deployment of offshore receivers.

5.3 Results

Of a total of 193 Greenland sharks tagged at 6 coastal locations, 155 individuals (101 males, 54 females [mean TL = 2.65 ± 0.48 m]) were detected between 65° and 72° latitude by 153 acoustic receiver stations deployed across 6 distinct coastal and offshore receiver arrays (**Fig. 5.1, Table 5.1**). In total, 88,009 shark detections were recorded across all arrays between August 8, 2011 and September 27, 2018, hereby referred to as the study period. Per receiver array, a mean of 9,156.0 ± 13,628.0 detections was recorded (*range = 2-33,046*), with the majority of detections recorded by inshore receivers (mean = 622.0 ± 1,353.0 detections/receiver) in coastal arrays (*range = 94-33,046*), compared to those deployed in the offshore (mean = 152.0 ± 296.0 detections/receiver) (*range = 2-1,754*).

5.3.1 Offshore presence

The three offshore arrays (ABO, DST, and QIK) recorded the presence of 55 unique individuals (33 males, 22 females [mean TL = 2.66 ± 0.49 m]) over the course of their consecutive 3 y deployments (Nov 2015 – Sept 2018; **Fig. 5.2**). Detected individuals included sharks tagged in 5 coastal locations, with large variation in the proportion of sharks detected relative to the total number of animals tagged at each location: Cumberland Sound (4% *of total tagged*, *n=23*), Grise Fjord (58%, *n=12*), Resolute Bay (40%, *n=15*), Scott Inlet (33%, *n=81*), and Tremblay Sound (23%, *n=62*). The minimum time at liberty prior to first being detected in the offshore was 61.61 d for a shark tagged in Scott Inlet in 2015, compared to a maximum time at liberty prior to offshore detection of ~6.37 y for one individual tagged in Cumberland Sound in 2011 (**Fig. 5.2**).

Sharks were detected on offshore receivers across ten months of the year, with no individuals detected in either September or October (combined data from 2015-2018 and accepting different offshore array configurations; **Fig. 5.3**). The absence of detections in September/October was bounded by low numbers of detected individuals in July, August, and November (mean = 0.9 ± 1.61 individuals/month detected across the entire offshore array for the 3-y deployment period). Over the remaining 7 months, a mean of 6 ± 5.74 individuals was detected per month, with non-recurrent peaks in abundance recorded in December 2016 (*n=14*), January 2016 and 2017 (*n=11, n=17, resp.*), May 2017 (*n=17*) and June 2018 (*n=13*). Interannual variation in the monthly detection rates of sharks reflected changes in the number of arrays present across each detection year and the number of sharks available for detection (see **Table 5.1** for array deployment and retrieval dates). As expected, months with the highest recorded shark abundance corresponded to years when multiple offshore arrays were deployed (39 sharks were detected when ABO, DST, and QIK were deployed simultaneously in 2017; **Fig. 5.3**). Minor differences in the monthly number of individuals detected by each array across deployment years were also observed (*e.g.*, peak detection rates for ABO occurred in May of 2017 *vs.* in June of 2018, **Fig. 3**), despite annual variations in array deployment period (Note: no offshore receivers were present prior to the first deployment of the DST array in September 2015; **Fig. 5.3**).

When considering hotspots of occurrence of sharks in the offshore relative to monitoring effort, the highest number of tagged individuals were detected in the ABO array located in the southeastern portion of Baffin Bay in the vicinity of the Disko Fan Conservation Area, ~213 km off the coast of Sisimiut, Greenland (DFO, 2008b).

Specifically, most sharks were detected on four gates in the ABO array (Nar01, Nar02, Nar03, Nar04), located along the eastern border of the fishery closure (**Fig. 5.1**). In 2017, sharks from 5 capture locations were detected on gate Nar03, with the highest annual detection rate recorded on southernmost gate, Nar04 (*n=15 individuals*). A second shark hotspot was observed near the easternmost stations in the DST array, located south of the closure and spanning the mouth of a deep-water channel connecting southern Baffin Bay to the Davis Strait (**Fig. 5.1, 5.4**), with 23 individuals detected on 1 receiver (C6) in 2017 (**Fig. 5.4**). The remaining gates in the ABO array, situated along the western continental slope of Baffin Bay (**Fig. 5.1**), recorded only 3 sharks on 2 receivers (of 17 total receivers) across 3 y (**Fig. 5.4**). Similarly, only 2 individuals were detected by receivers in the offshore QIK array (**Fig. 5.4**), located in line with the western shelf gates of the ABO array.

Of the 56 receivers comprising the 3 offshore arrays, 21 receivers recorded the presence of tagged sharks. Individual tagged sharks were typically detected by a small number of offshore receivers per year (mean = 1.67 ± 0.98 receivers/y) and by a mean of 2.6 ± 1.71 receiver stations across the entire 3 y study period (**Fig. 5.5**). More than half of the tagged population were, however, redetected in the offshore across multiple years (56%, *n=55*; 20 sharks were detected over 2 y [*n=176 sharks tagged by end 2017*], 9 were detected over 3 y [*n=145 sharks tagged by end 2016*], and 2 were detected over 4 y [*n=121 sharks tagged by end 2015*]), resulting in an average of 1.8 ± 0.85 detection years per individual (**Fig. 5.5**). A total of 24 individuals were recorded only once by offshore arrays, representing 14% of the total tagged sharks available for detection in the offshore across 2 study years (*i.e.*, those tagged by end 2017; *n=176*) (**Fig. 5.5**).

Sharks detected over multiple years (*n=31 individuals*) demonstrated a high degree of overlap in the offshore locations visited across years, with 19 sharks (61%) visiting receivers in the same gate across multiple detection years (**Fig. 5.6**). The gates with the highest frequency of individuals redetected across multiple years were gates C6 (*n=9 individuals*; DST array) and Nar04 (*n=8 individuals*; ABO array) (**Fig. 5.6a**). While not detected on precisely the same gates across years, the remaining sharks (*n=12*) were mostly detected within the same offshore region (gates C5-C6 and Nar01-Nar04) throughout the study period (**Fig. 5.6b**).

5.3.1.1 Transient movement behaviour in offshore waters

The *glatos* 'detection_events' function reduced our dataset of 3,652 offshore detections to 190 detection events within a maximum interval of 7 days (604,800 sec). Among the detection events calculated, the average number of detections recorded was 19 ± 32.37 with a mean event duration of 31,231 ± 103,830.8 seconds (~8.68 h).

The mean duration of detection events varied by receiver gate, with the longest event durations recorded by gates in southeastern Baffin Bay (Nar01-Nar04, C5-C6; **Table 5.2**). Receiver gates located along the western side of Baffin Bay had detection events that were considerably shorter by comparison and recorded fewer overall detections and detection events (Baff03, Baff06, C3, C4, Q02, Q05; **Table 5.2**).

Given the nominal delay of our acoustic tags and the average swimming speed of Greenland sharks (Watanabe et al., 2012), the minimum predicted time for an individual to transit on a linear path through the widest point of the detection radius of a receiver was calculated to be 4,717.65 sec (~1.31 h) with an expected 14.15 detections at detection efficiency of 60%. This estimated minimum transit time indicates that sharks detected by gates C3 and C4 were transiting past receivers at the time of detection. Sharks detected by gates Baff06, C5, Nar01, and Nar03 were likely also exhibiting transient movements when considering the additional time that might be required for sharks to undertake vertical displacements while transiting through the detection radius. For 3 receiver gates (Nar04, Nar02, and C6) that were located in the two high activity regions, detection events were much longer in duration than our minimum estimate, indicating that sharks were temporarily resident at those sites.

5.3.2 Patterns in coastal abundance

Within the 5 coastal arrays, 138 sharks (91 males, 47 females [mean TL = 2.62 ± 0.48 m]; 72% of total tagged, *n=193*) were detected throughout the 7 y study period: Resolute Bay (40% of tagged sharks detected, *n=15*); Tremblay Sound (87% detected, *n=62*); Scott Inlet (96% detected, *n=81*); Cumberland Sound (39% detected, *n*=23); and Home Bay (100% detected, *n=1*). In terms of seasonality, sharks were detected in coastal arrays primarily during and just after tagging periods with low detection rates in subsequent months and years. For example, peaks in monthly abundance in Scott Inlet (mean ± SD = 12.6 ± 6.29 individuals/month; ASI array) were recorded in September and October between 2012 and 2016. Outside of peak tagging periods, a mean of 2.86 ± 1.66 individuals/month was observed in in July, August and November across all years. This pattern mirrored the detection rates of sharks recorded in September and October of 2017 (2.5 ± 0.71 individuals/month) when no tagging took place in Scott Inlet. Equally, a peak abundance of 22 ± 8.45 tagged individuals/month was observed in August (2017-2018) in Tremblay Sound (ATS array) during active tagging operations compared to a mean of 2.4

± 1.20 individuals/month recorded over the non-tagging detection months of July, September, and November.

5.3.3 Coastal-offshore seasonality

Greenland sharks were detected throughout the year across both offshore and coastal systems in Baffin Bay, however, apparent segregation in the timing of shark presence was observed between the two environments. While sharks were detected across 10 months of the year by offshore receiver stations (ABO, DST, and QIK arrays; **Table 5.1**), shark presence in coastal habitats was strongly tied to the summer ice-free months between July and November (**Fig. 5.7**). This trend was consistent for all 4 coastal receiver arrays (ATS, ASI, QIK, and ACS arrays) across the 7-y study period. The distinct seasonal pattern in coastal waters was matched by a simultaneous decrease in the abundance of sharks detected by offshore receivers throughout the same 4-month period over the 3 consecutive years of monitoring (**Fig. 5.3**).

When examining the seasonal transition of sharks detected in the coastal trough off of Qikiqtarjuaq and the offshore arrays over the same 3 y period, the highest number of sharks were recorded in the offshore between the months of January and June (mean ± SD = 2.62 ± 3.16 individuals/month [*range = 1-21*]). Sharks were primarily detected by the eastern portion of ABO (gates Nar01-Nar04) and central DST (C6) (**Fig. 5.8a**). During the ice-free summer months between July and October, 73% of detected individuals (*n=15*) were recorded on receivers in Qikiqtarjuaq's coastal trough, resulting in a detection rate of 1.07 ± 0.27 individuals/month (*range = 1-2*) for the entire 4-month period (**Fig. 5.8b**). In the latter months of November and December, shark detections were concentrated in the offshore along Baffin Bay's eastern shelf in the vicinity of the fishery closure (frequency of detected individuals increased to an average of 1.85 ± 1.87 individuals/month; *range = 1-9*) (**Fig. 5.8c**). The trend in shark movements observed at this finer scale supports the general seasonal pattern observed for all tagged sharks throughout Baffin Bay (**Fig. 5.7**).

5.3.4 Individual-level movements and efficiency of offshore arrays

Of the total 155 sharks detected, 48 individuals exhibited movements between multiple receiver arrays (*i.e.,* ≥ 2 coastal arrays, ≥ 2 offshore arrays, or on both coastal and offshore arrays) (**Fig. 5.9**). Based on the number of years in which an individual was detected in coastal waters, two distinct groups of sharks were identified.

Group 1 contained sharks that were either never detected in coastal waters or that were only detected in these systems once (*i.e.,* in 1 y). This group included 66.7% of the total sharks considered (*n=32*), with 8 sharks (17% of total) detected only in the offshore (**Fig. 5.9**). The remaining sharks in this group were first detected in the coastal array in which they were tagged, followed by the offshore (with one exception; shark ID: 101007, **Fig. 5.9a**). Despite being undetected by coastal arrays, sharks detected only in the offshore were, nonetheless, tagged in coastal regions and therefore demonstrate the same transitional movement exhibited by the remaining cohort of sharks in this subset (**Fig. 5.9a**). Time at liberty between tagging/release and the first recorded detection ranged from 1-1,534 d (~4.2 y) for sharks in group 1, however, longer durations were driven by delays between the date on which sharks were tagged and the later deployment of offshore arrays. Sharks that exhibited the longest periods prior to detection were those that were only detected in the offshore (with the exception of shark ID: 101007). The majority of these sharks were tagged in coastal locations that did not have active arrays present at the time of tagging/release (Grise Fjord [*n=2 individuals*], Resolute Bay [*n=1 individual*], Tremblay Sound [*n=4 individuals*], and Cumberland Sound [*n=1 individual*]; **Fig. 5.9a**).

Group 2 contained 16 individuals (33% of total) that were detected in coastal regions across multiple years, including 2 sharks that were detected only in coastal waters and 6 that were detected by more than one distinct coastal array (**Fig. 5.9b**). Across these 16 individuals, 17 coastal absence periods were identified (*i.e.,* periods of time between consecutive events of temporary coastal residency) (**Fig. 5.9b**). During these coastal absence periods, tagged sharks were detected by offshore arrays 76% of the time (*n=17 events*) (**Fig. 5.9b**). In contrast, only 4 coastal absence periods (24%, *n=17 events*) were identified wherein sharks were not detected by offshore receivers (representing 4 individuals; **Fig. 5.9b**).

A subset of individuals in group 2 demonstrated predictable coastal-offshore transitional movements which repeated for up to a maximum of 4 years (shark ID: 101632, 101545, 101432; **Fig. 5.9b**). One individual demonstrating a similar pattern remained undetected in coastal waters in 2017, resulting in a longer perceived duration of offshore residence between 2016 and 2018 (shark ID: 101544; **Fig. 5.9b**). A number of sharks demonstrated movement patterns similar to those in group 1, where individuals were detected exclusively in coastal waters for the first 2-3 detection years (before the deployment of the offshore arrays), after which they were detected in the offshore over the remainder of the study period (shark IDs: 101428, 101423, 101315, 101224; **Fig. 5.9b**). Nearly all sharks in this group were tagged in Scott Inlet, where they were detected within the first 3 d following release (69%, *n=16 individuals*; **Fig. 5.9b**). Pre-detection periods for the remaining individuals ranged from 9-22 d (25%, *n=16*), with one exception - a shark tagged in Resolute Bay with a pre-detection period of 1,081 d (~3 y) (shark ID: 101943; **Fig. 5.9b**).

5.4 Discussion

To date, knowledge of the movements of Greenland sharks, particularly over long durations, is limited. The data available have primarily been derived from short-term tracking studies lasting several hours to several months, providing insight into fine-scale horizontal (Skomal & Benz, 2004) and vertical movement behaviours (Campana et al., 2015a; Gallant, Rodriguez, Stokesbury, & Harvey-Clark, 2016; Harvey-clark, Gallant, Block, & Myers, 2005) and evidence of large-scale displacements exhibited by this species (Campana et al., 2015a; Fisk, Lydersen, & Kovacs, 2012a; Hussey et al., 2018). The few studies that have examined the movements of Greenland sharks in offshore waters have used geospatial data collected by pop-off satellite archival tags (PSATs) (Campana et al., 2015a; Fisk, Lydersen, & Kovacs, 2012b; Hussey et al., 2018). While these tags archive high resolution vertical movement data, their application for examining the horizontal movements of deep-water animals is limited to straight line trajectories interpolated between the location of the animal's release and the location of the satellite tag's first successful transmission to ARGOS satellites following it's programmed release (Edwards et al., 2019). By attaching several mrPATS (mark-report satellite tags) to individual Greenland sharks and setting them to release in sequence, one study provided the first course-scale movement trajectory for this species (Hussey et al., 2018). While this method improved upon resolution of previously available horizontal movement records (providing data collected over a 2.5-month period), the longevity of monitoring possible using acoustic transmitters far exceeds that of satellite telemetry approaches (up to 10 y; VEMCO product specifications, https://vemco.com). The current study provides the longest period of continuous monitoring of Greenland shark movements (up to 7 y) to date. It is also the first to identify repeated seasonal transitions between inshore and offshore habitats and to document evidence of inter-annual site fidelity exhibited by individual sharks in the offshore.

5.4.1 Offshore presence and movements

In just over 3 y of monitoring and with limited spatial coverage of offshore receivers, we detected 55 unique sharks, all tagged and released in coastal systems across a wide range of latitudes. The data collected for these individuals demonstrated similarities in behaviour and habitat use among sharks tagged throughout the Eastern Canadian Arctic and highlights the significance of offshore regions for this species.

While sharks were detected across 38% of offshore stations, notable temporal and spatial variation in the number of individuals detected throughout the offshore was observed. In both cases, this variation was partly due to changes in the number of receivers actively deployed in offshore arrays. Temporal analyses showed that greater numbers of sharks were detected when the presence of all arrays coincided (*i.e.,* in 2017). During this time, monthly offshore abundance increased, and sharks were detected throughout more months of the year relative to periods of time when fewer arrays were present. Similarly, spatial differences in shark abundance were biased by the number of stations deployed in each array, where the arrays with the greatest spatial coverage showed a higher efficiency for detecting tagged individuals (**Fig. 5.4**).

Published studies incorporating detection data collected over multiple years of continuous acoustic telemetry monitoring are still relatively rare. This is largely due to logistical challenges faced by individual researchers such as the inability to fund and manage extensive receiver networks over long durations, the complexity of long-term or large-scale data generated by spatiotemporally expansive arrays, as well as a lack of knowledge of the appropriate time-scales over which arrays should be maintained (Krueger et al., 2017). However, with the expansion of multi-national organizations like the Ocean Tracking Network (OTN; www.OceanTrackingNetwork.org) that provide equipment, resources and funding for numerous telemetry projects, a growing number of researchers have begun redeploying acoustic arrays over extended periods. Multi-year array deployments have consequently allowed the collection of long-term movement data (Meyer, Papastamatiou, & Holland, 2010; Papastamatiou, Friedlander, Caselle, & Lowe, 2010) and the optimization of array design for improved detection efficiency (Clements, Jepsen, Karnowski, & Schreck, 2005; Heupel, Semmens, & Hobday, 2006). Observed differences in detection efficiency resulting from changes in the design of our offshore arrays highlight the importance of array optimization for maximizing the collection of movement data. However, it is important to note that despite the variability in array design that occurred during the present study, our results demonstrate a relatively consistent seasonal pattern in the offshore presence of Greenland shark across the 3-y monitoring period.

When examining the spatial distribution of shark detections, we observed a bias towards the southeastern portion of Baffin Bay in the vicinity of a fishery closure known as the Disko Fan Conservation Area (DFO, 2008b). In 2011, this area was designated an

Ecologically and Biologically Significant Area (EBSA) based on its diverse, and well established deep-water coral communities, bathymetric and oceanographic complexity, and sea-ice characteristics that allow the overwintering of narwhal and other marine mammals (*i.e.*, persistent leads through winter pack ice) (DFO, 2008b; Hiltz, Fuller, & Mitchell, 2019). This productive deep-water ecosystem is therefore home to many prey species potentially targeted by Greenland sharks, including marine mammals whose seasonal presence in this region overlaps with that of many Greenland sharks monitored during this study. Other seasonal diversity, abundance, and activity hotspots have been identified for marine megafauna throughout Baffin Bay and the Canadian Arctic in locations where favorable environmental and oceanographic conditions lead to spikes in primary productivity, resulting in increased benthic and pelagic biomass (Yurkowski et al., 2018). This may help to explain trends observed in the current study, wherein receivers in the Disko Fan region detected a disproportionately high number of individuals compared to the remaining offshore stations and had the most repeated visitations of individuals across multiple years.

These results also indicate that a small subset of sharks exhibited some evidence of site fidelity to the Disko Fan region. While mark-recapture and genetics studies have revealed natal and sex-specific reproductive philopatry in a number of shark species (Feldheim et al., 2014; Mourier & Planes, 2013; Sims, Nash, & Morritt, 2001; Tillett, Meekan, Field, Thorburn, & Ovenden, 2012), evidence of individual-level site fidelity (return to a study region) obtained via electronic tagging methods are much more limited (Hueter, Heupel, Heist, & Keeney, 2005; Jorgensen et al., 2010; Kessel et al., 2014). Previous studies on elasmobranch species have identified site fidelity to regions thought to be associated with mating (Feldheim, Gruber, & Ashley, 2002; Pratt & Carrier, 2001), giving birth (Kessel et al., 2014), and feeding (Driggers et al., 2014; Espinoza, Farrugia, & Lowe, 2011; Lowe, Wetherbee, & Meyer, 2006). Additional evidence also suggests that seasonal patterns of site fidelity may not be restricted to alternating movements between two discrete locations. For example, white sharks (*Carcharodon carcharias*) have been shown to demonstrate highly predictable movements wherein individuals returning from oceanic migrations visit an entire network of coastal foraging hotspots with locations that vary among genetically distinct clades (Jorgensen et al., 2010).

Based on our findings, we propose that Greenland sharks may use the Disko Fan region as a winter foraging ground and suspect that individual sharks are likely to exhibit a similar level of site fidelity to other high-biomass marine regions across Baffin Bay, as illustrated by recurrent summer visitations to coastal fjord systems such as Scott Inlet, Nunavut (Edwards et al., unpublished; see **Chapter 5.4**). Moreover, given interannual variability in the return of individuals to specific coastal (Edwards et al., unpublished; see **Chapter 5.4**) and offshore regions **(Fig. 5.6)**, along with the detection of unique individuals by multiple coastal arrays (**Fig. 5.9**), we predict that the movement patterns of Greenland sharks may include periods of temporary residency in a number of foraging hotspots, similar to observed white shark behaviours (Jorgensen et al., 2010).

While foraging suitability is likely a strong motivating factor driving the return of sharks to these regions, the locations of mating and birthing grounds used by this species are, as yet, unknown. Following the spatial management ideologies used to restrict anthropogenic disturbances within this fishery closure (DFO, 2008b), we suggest that further studies that can identify additional regions of high predator density and specific locations of site fidelity for Greenland sharks (particularly regions that may be significant for shark reproduction) would facilitate the implementation of spatial management approaches that could ensure the stability of Arctic marine communities and prevent population declines in this species.

In contrast to receivers located in southeastern Baffin Bay, tagged sharks were detected by only 4 receiver stations among the 9 gates deployed along ~760 km of the basin’s western continental shelf (ABO and offshore QIK arrays), resulting in the detection of 4 individuals in total. This outcome seems unlikely, given the high numbers of detections recorded in coastal fjords along the same stretch of coastline. This discrepancy indicates that Greenland sharks are likely either transiting along the coastline at a close proximity to the shore or are entering coastal systems directly from offshore waters. These potential behaviours would contrast those exhibited by Greenland halibut (*Reinhardtius hippoglossoides*) for which the array was designed, wherein fish are detected and targeted by commercial fisheries as they move along the shelf edge (DFO, 2013). Both behaviours have, however, been observed in other shark species that either preferentially avoid (*e.g.,* common thresher sharks, *Alopias vulpinus*; Cartamil et al., 2010) or make use of shallow waters while moving along the continental shelf (*e.g.,* porbeagle, *Lamna nasus*, and school shark, *Galeorhinus galeus*; Pade et al., 2009; West & Stevens, 2001). Given the frequent use of offshore waters and seasonally alternating pattern in coastal and offshore detections observed in this study (**Fig. 5.9b**), we speculate that Greenland sharks likely transit through offshore regions while moving between the distinct coastal fjords along the borders of Baffin Bay.

While the majority of tagged sharks were detected in offshore waters over multiple years, individuals were detected by very few offshore receiver stations on average and were also detected a low number of times by each. These factors suggest that tagged sharks demonstrated a degree of transient movement when travelling throughout offshore waters, spending limited time in each location along their movement path. Fine-scale behaviours exhibited during the large-scale displacements of marine fishes are, in general, difficult to study and are therefore not well understood (Comeau, Campana, & Castonguay, 2002). However, tracking studies have provided records for many large, mobile marine species that have been shown to exhibit directed movements over vast distances in relatively short periods of time (Domeier & Nasby-Lucas, 2008; Hearn et al., 2016; Matthews, Luque, Petersen, Andrews, & Ferguson, 2011). This behaviour has also been previously reported for Greenland sharks that were found to travel distances of several hundred kilometers through open-water regions in just a few months (Campana, Fisk, & Peter Klimley, 2015b; Hussey et al., 2018). Based on the mean duration of offshore detection events reported in this study, we propose that the movement of tagged sharks in offshore waters appears to be similarly transient in nature with the exception of key locations within the fishery closure. This could indicate that sharks in this study were frequently detected while undertaking directed movements between regions of high activity where they demonstrate temporary residency. Despite the presumed negative correlation between transient movement and the frequency of shark detections, we predict that this behaviour might increase the likelihood of sharks encountering offshore receivers and may have had a positive influence on the detection efficiency of our offshore arrays.

5.4.2 Seasonality in coastal and offshore presence

There is currently a limited understanding of Greenland shark distribution and population abundance throughout the species' range. Primary records have been produced largely by fisheries-dependent methods, including commercial and historical bycatch records, and shark catches reported by exploratory fisheries surveys and commercial stock assessments for targeted Artic species such as the Greenland halibut (*R. hippoglossoides*) and Northern shrimp (*Pandalus borealis*) (Edwards et al., 2019). While these records are essential to our current knowledge of Greenland shark distribution, these data are likely biased by fishing gear type, set duration, and the timing of fishing efforts which are all thought to affect the relative frequency and abundance of Greenland shark bycatch (Bryk et al., 2018). As supported by our findings, numerous sources from all three of these categories confirm the presence of Greenland sharks in the inshore regions of Baffin Bay during the ice-free summer period (July to November). Inshore multi-species surveys conducted by Fisheries and Oceans Canada (DFO) between 2010 and 2017 reported the incidental capture of a median 11 Greenland sharks per year (*range = 0-47*) over a median of 29 annual sets (*range = 5-43*) (Bryk et al., 2018). These efforts demonstrated Greenland shark presence in coastal waters across a range of latitudes along the eastern shores of Baffin Island, from the northern community of Pond Inlet (2017), ranging south to Clyde River (2011) and Scott Inlet (2012-2015) and finally to Qikiqtarjuaq (2017), Merchant's Bay (2011), Cumberland Sound (2010-2014), and Pangnirtung (2017).

Catch data from exploratory fisheries for Greenland halibut have also provided substantial documentation of the summer presence of Greenland sharks in inshore areas.

Exploratory fisheries conducted between July 1st and Nov 10th in deep-water (>500 m) coastal areas near Qikiqtarjuaq (Hathaway 1993) and Davis Strait, Resolution Island, and Cumberland Sound (Northlands Consulting 1994) reported high numbers of Greenland sharks caught by a variety of gear types (52 sharks in 11 gillnet sets in 1993) (Treble & Stewart, 2010). Similar reports were produced by longline fisheries and fishery training courses conducted in Cumberland Sound in 2003 (12 sharks caught over 10 longline sets; Walsh 2003) and 2009 (570 sharks caught in 55 sets; Treble & Stewart, 2010) as well as commercial bycatch records dated from 1987 to 2006, in which annual reported captures ranged from 4 to 220 individuals ($median = 60$) over a total number of reported longline sets between 74 and 1,782 ($median = 601$) (DFO, 2008a). The importance of inshore regions for Greenland shark summer distribution in northern Baffin Bay (NAFO subarea 0) was also proposed following exploratory longline fisheries conducted in late September near Grise Fjord, Qikiqtarjuaq, Arctic Bay, and Resolute, during which Greenland shark presence was said to be ubiquitous (Wheeland & Devine, 2018).

Recently, surveys conducted using Baited Remote Underwater Video systems (BRUVs) provided the first fisheries-independent estimates of the relative abundance of Greenland sharks in the Canadian Arctic and identified shark presence in coastal systems during the open-water period (Devine et al., 2018). Like the majority of the aforementioned methodologies, BRUVs surveys have thus far been restricted to the summer months between July and September (2015 & 2016) when the absence of sea-ice provides access to these coastal waters.

Finally, a tracking study that deployed multiple pop-off archival satellite tags on Greenland sharks to produce course-scale movement trajectories also identified the summer use of coastal fjords by the species, in addition to demonstrating temporary coastal residency and large-scale migrations between inshore systems in northeast Devon Island (Canada) and northwest Greenland (Hussey et al., 2018).

As our findings suggest, the presence of Greenland sharks in coastal systems appears to peak in the summer months, relative to the occurrence of sharks present in these systems during the winter, indicated by catch records from experimental and community-based winter fisheries (Idrobo, 2008; Walsh, 2018). Importantly, these records demonstrate that Greenland sharks are, in fact, present in at least some coastal systems year-round. However, evidence to support the presence of sharks in coastal systems in the winter is far less abundant due to annual coverage by sea ice which limits access to commercial vessels, in addition to a lack of winter ice-based fisheries in many coastal communities.

To date, only one telemetry study has successfully tracked the coastal movements of Greenland sharks under ice, taking place in the Strathcona Sound and Victor Bay region between the 16th to the 28th of May, 1999 (Skomal & Benz, 2004). While confirming the coastal presence of Greenland sharks in the winter months, the short duration of this study does not indicate the nature of residency (*i.e.,* timing, duration) or provide evidence of return behaviour to the region.

Bycatch records from winter fisheries in Cumberland Sound (DFO, 2008a) and Scott Inlet (Walsh, 2018) both report catching high numbers of Greenland sharks using deep-water longlines set through the ice. However, a comparison of historical catch records from summer and winter fisheries in Cumberland Sound indicate a relative increase in the coastal presence of Greenland sharks during the summer months.

Specifically, an open water summer longline fishery conducted in 2009 reported an average catch rate of 6.3 sharks per 1,000 hooks (570 total individuals) (Young 2010) while a mere 1.1 sharks per 1,000 hooks (ranging between 0.4 and 2.9 sharks/1,000) were reported as bycatch in the Pangnirtung winter Greenland halibut fishery between 1987 and 2006 (Bryk et al., 2018; DFO, 2008a). Despite reporting relatively stable catches of Greenland halibut throughout this winter fishing season, which typically runs from late January/early February to the end of April/early May, local fishermen also suggest that Greenland shark abundance varies cyclically (Idrobo, 2008). High numbers of Greenland sharks are reportedly observed early in the season, followed by a no-shark period lasting until the end of March, and terminated by a sudden resurgence lasting until the end of the fishing season (Idrobo, 2008). Inuit fishermen from this community have proposed three explanations for the apparent seasonal pattern which include:

a) Greenland sharks follow a natural migration pattern in which Cumberland Sound is suspected to serve as a summer habitat before their departure to deeper offshore waters in the late summer.

b) Greenland sharks are permanent residents of Cumberland Sound – a proposition based on high numbers of Greenland sharks sighted near the surface in the open-water period as well as winter incidental captures.

c) Sharks are lured to coastal areas by discards and offal produced by fishing practices. The amount of bait left soaking is also thought to have a positive correlation with shark abundance.

Exploratory fishing efforts for another community-based winter fishery north of Cumberland Sound in the Scott Inlet/Sam Ford fjord system also reported significant

Greenland shark bycatch, with a total of 29 Greenland sharks (mean TL = 2.94 ± 0.13 m) caught over 42 longline sets in late May of 2007 (Walsh, 2018). This contradicts the pattern observed in this study, where tagged Greenland sharks were only detected in Scott Inlet between July and November (**Fig. 5.3**). Specifically, over the entire study period, tagged sharks were found to be invariably absent from all four inshore arrays (ATS, ASI, QIK, ACS) throughout the ice-covered period from December to June (**Fig. 5.3**). This leads us to pose the following question: If a subpopulation of Greenland sharks that displays year-round coastal residency exists, why has this behaviour not been exhibited by any of our tagged individuals? Alternatively, is it possible that Greenland shark populations are divided into behavioural subcategories that temporally segregate their use of coastal and offshore habitats? While we may not be currently able to answer these questions with absolute certainty, we can speculate on a few possible explanations.

Firstly, we suggest that, given the short-term residence displayed by tagged individuals in all four coastal systems, and their ubiquitous absence throughout the winter months, it is unlikely that Greenland sharks are permanent (*i.e.*, your-round) residents of coastal systems. Our large sample size, frequent tagging efforts, and range of tagging locations also suggest that it is unlikely that permanent residency, if displayed by a significant portion of the population, would not have been captured by our study. Alternatively, it is believed that Greenland sharks are highly transient, but display some evidence of site fidelity to particular coastal systems (Edwards et al., unpublished; see **Chapter 5.4**) and offshore regions. This study also suggests that Greenland sharks may alternate visitations to multiple coastal systems, as there were several instances where sharks were detected by coastal arrays other than the one in which they were tagged (**Fig. 5.9**).

Second, we propose that, if Greenland sharks display temporal habitat segregation, then the timing and location of tagging efforts in our study may be a potential source of sampling bias. In other words, we suspect that by tagging sharks exclusively in coastal waters in the summer, we may not have been present at the same time as individuals that follow the alternate seasonal movement pattern, thereby resulting in the absence of sharks displaying temporary winter coastal residency in our tagged population. To address this concern, additional efforts must be made to tag sharks captured through the ice by inshore winter fisheries. By comparing the seasonal movements of these individuals to our existing tagged population, we might verify the existence of behavioural subcategories within the population. It is important to note that tagging expeditions such as these are logistically challenging (and have therefore been limited to date) given the difficulty of accessing these coastal systems during the winter, as well as the additional physiological stress imposed on captured animals that must be hauled out of the water through ice-fishing holes for the tagging procedure to be conducted. However, successful tagging of Greenland sharks through winter sea ice is possible (Skomal & Benz, 2004; N.E. Hussey, pers. comm.) and should be considered by future studies.

Another important consideration is the possible explanation for the potential existence of temporal habitat segregation in this species. Previous research has suggested that, due to the simultaneous occurrence of both size classes in both the offshore waters and deep-water fjords of Greenland (Nielsen, Hedeholm, Simon, & Steffensen, 2014;

Yano, Stevens, & Compagno, 2007), habitat/depth segregation between juveniles and subadults based on size appears to be unlikely (Hussey et al., 2015). Furthermore, there appears to be no significant differences in the timing and occurrence of males and females in the coastal waters of Scott Inlet (Edwards et al., unpublished). We might therefore suggest the possibility of different dietary regimes within the population as a potential explanation for this apparent behaviour. While adult within-population differences in dietary specialization are relatively uncommon in the animal kingdom (*e.g.*, grizzly bears, *Ursus arctos;* M. A. Edwards, Derocher, Hobson, Branigan, & Nagy, 2011, and killer whales, *Orcinus orca;* Ford et al., 1998), ontogenetic dietary shifts are prevalent, particularly among sharks (Bethea, Carlson, Buckel, & Satterwhite, 2006; Hussey et al., 2012; Taylor & Bennett, 2008). Evidence of ontogenetic dietary shifts have also been observed for the Greenland shark (Nielsen et al., 2019), as well as geographic variation in dietary preference (Fisk, Tittlemier, Pranschke, & Norstrom, 2002; MacNeil et al., 2012), although whether the latter evidence represents true natural variation is the subject of some speculation (Edwards et al., 2019). We therefore suggest the possibility that the seasonal presence of Greenland sharks in coastal systems may differ based on population-level differences in preference for prey species that differ in availability across seasons.

5.5 Conclusion

The multi-year movement records examined in this study provide insights on Greenland shark movements at an unprecedent temporal scale. Three years of shark detections in the offshore waters of Baffin Bay illustrate the predominant use of deep, offshore waters in the ice-covered winter period between November and June, with fewer offshore detections also recorded in July and August. Tagged sharks exhibited notable site fidelity to specific offshore activity hotspots, with contrasting transient movements throughout the remainder of monitored offshore areas. Greenland sharks were also detected in four coastal habitats across a seven-year period; however, these inshore detections were tightly restricted to the ice-free summer months between July and November.

Abundant bycatch records from commercial fisheries, exploratory fisheries surveys and commercial stock assessments, as well as abundance estimates from BRUVs surveys and satellite tracking data substantiate the high numbers of tagged Greenland sharks shown by this study to frequently visit coastal arrays during the summer months. However, contradictory to evidence of Greenland shark bycatch records from winter fisheries in Cumberland Sound (DFO, 2008a) and Scott Inlet (Walsh, 2018), and the mobile acoustic tracking of sharks under ice in the fjords of northern Baffin Island, tagged sharks were not detected by any of our coastal receiver arrays in the winter months. To explain this trend, we suggest that Greenland sharks may demonstrate a behavioural dichotomy wherein individuals belong to one of two subpopulations that are present in inshore waters exclusively in the winter or summer periods. We thereby attribute a lack of winter tagging efforts in coastal systems to the absence of temporary winter residents in our tagging population and propose these additional tagging efforts as a potential solution.

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TABLES/FIGURES

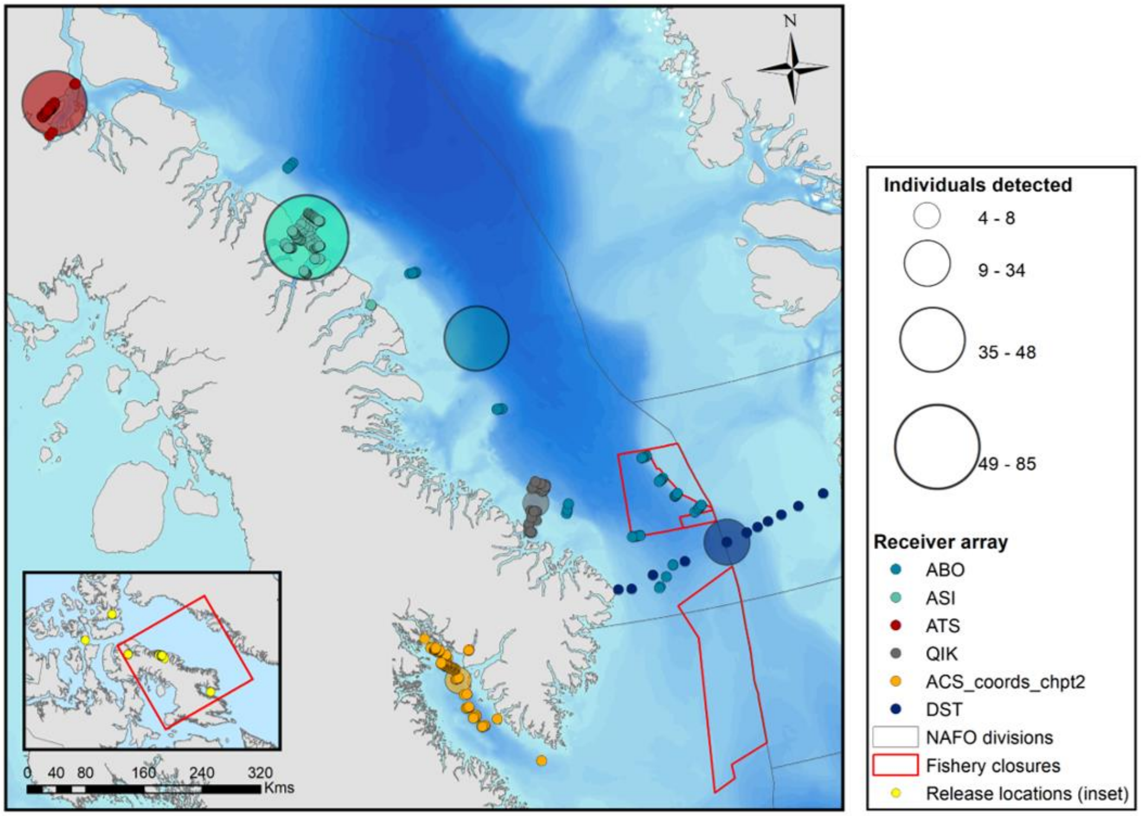

Figure 5.1 | Locations of acoustic receivers used to the monitoring the presence of tagged Greenland sharks deployed across four coastal regions of Nunavut (Eastern Canadian Arctic) and offshore Baffin Bay. Points are coloured by receiver array, where solid points represent the locations of individual receivers and semi-transparent points are scaled in size to represent the total number of individuals detected per array. Release locations of tagged Greenland sharks are depicted in the inset map.

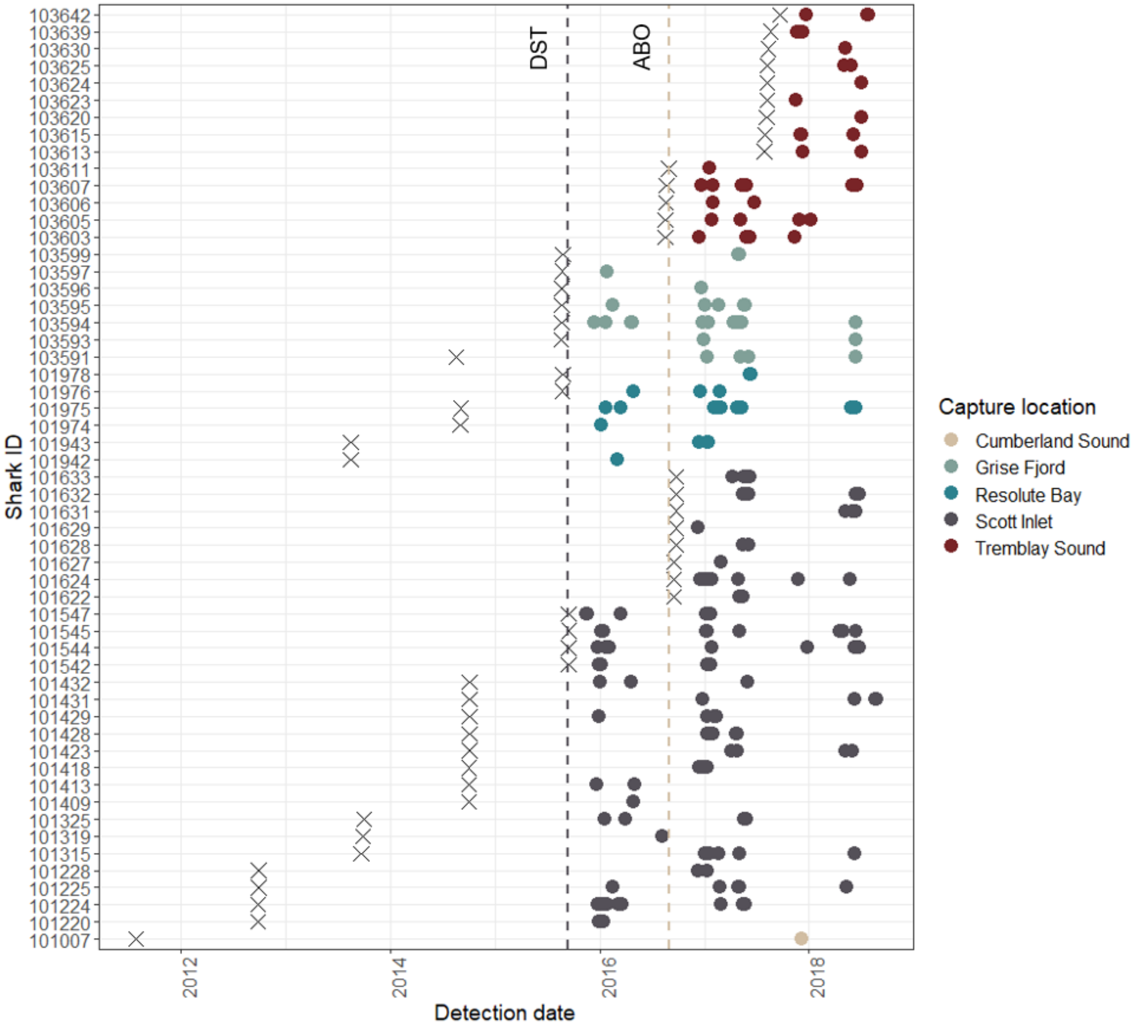

Figure 5.2 | Temporal distribution of Greenland shark detections recorded by acoustic receiver stations in offshore Baffin Bay (combined ABO, DST, and QIK arrays) listed by shark ID. Point colour denotes the capture locations of individual sharks and the date of tagging and release for each animal is marked by an ‘X’.

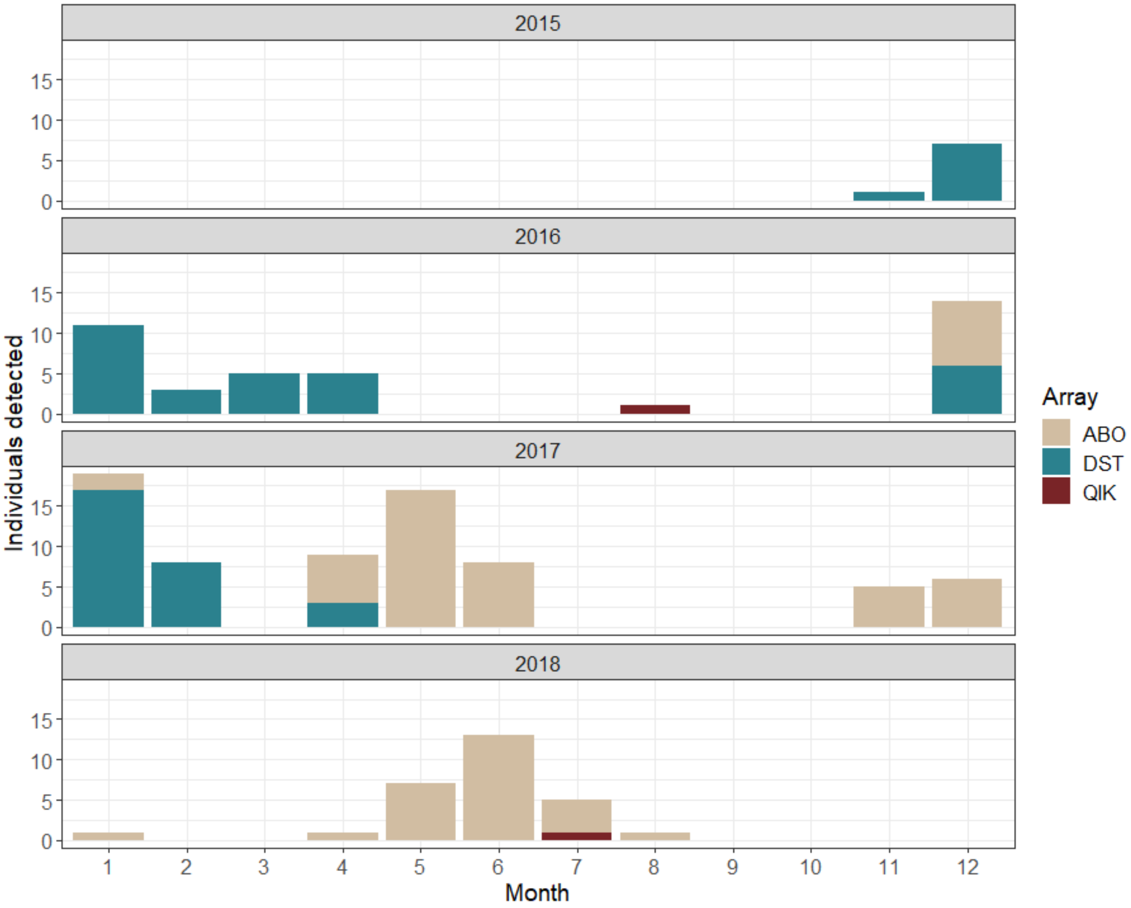

Figure 5.3 | Total number of tagged Greenland sharks detected by acoustic receiver stations in offshore Baffin Bay (ABO, DST, and QIK arrays) listed by month and year. Bar colour denotes the offshore array in which detections were recorded. It should be noted that initial array deployment dates limit the number of detections observed before September 2016 (ABO array first deployed 2016-08-31, DST deployed 2015-09-09, and QIK deployed 2015-10-07).

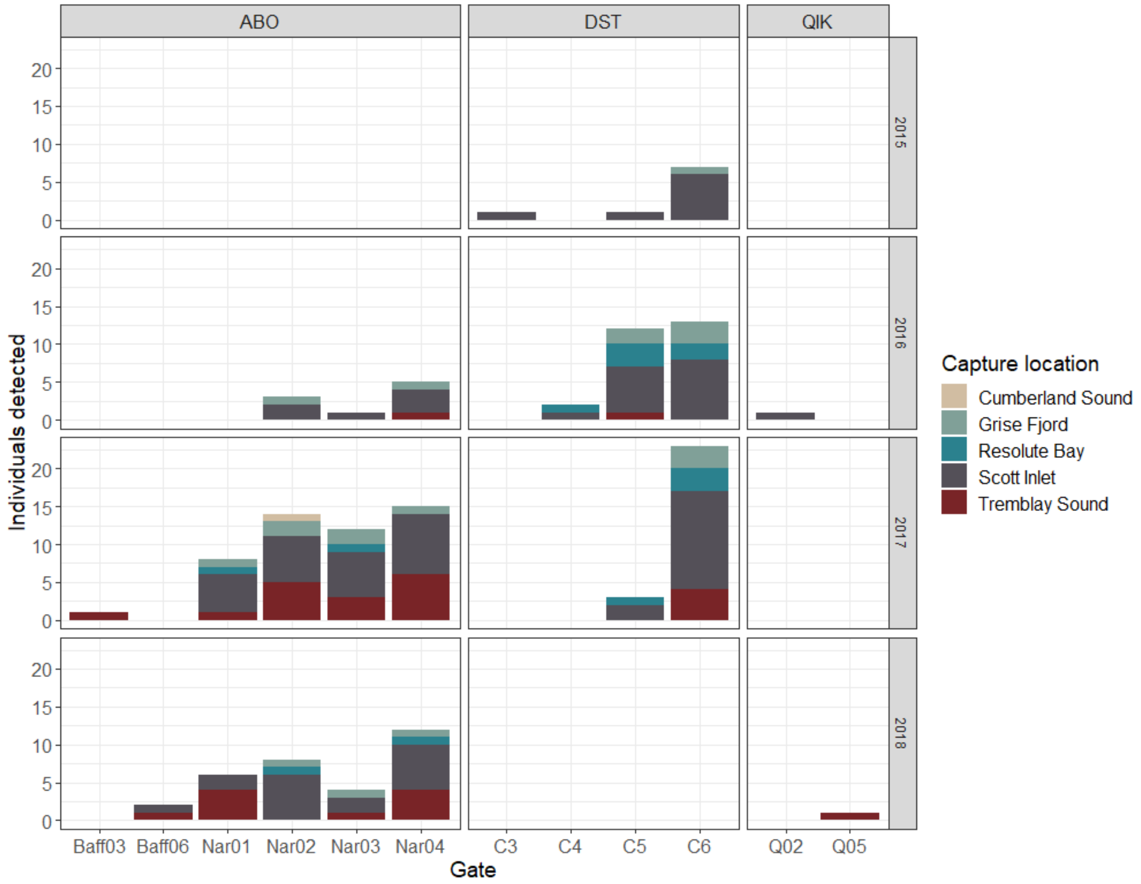

Figure 5.4 | Total number of tagged Greenland sharks detected by offshore acoustic receiver stations listed by receiver gate and grouped by array (ABO, DST, and QIK). Bar colour denotes the capture locations of detected individuals.

Figure 5.5 | Greenland shark detections recorded by acoustic receiver stations in offshore Baffin Bay (ABO, DST, and QIK arrays) listed by the identification number of tagged sharks, the number of offshore stations on which detections were recorded, and the monitoring year. Bar colour indicates the number of years detected in the offshore for individual sharks.

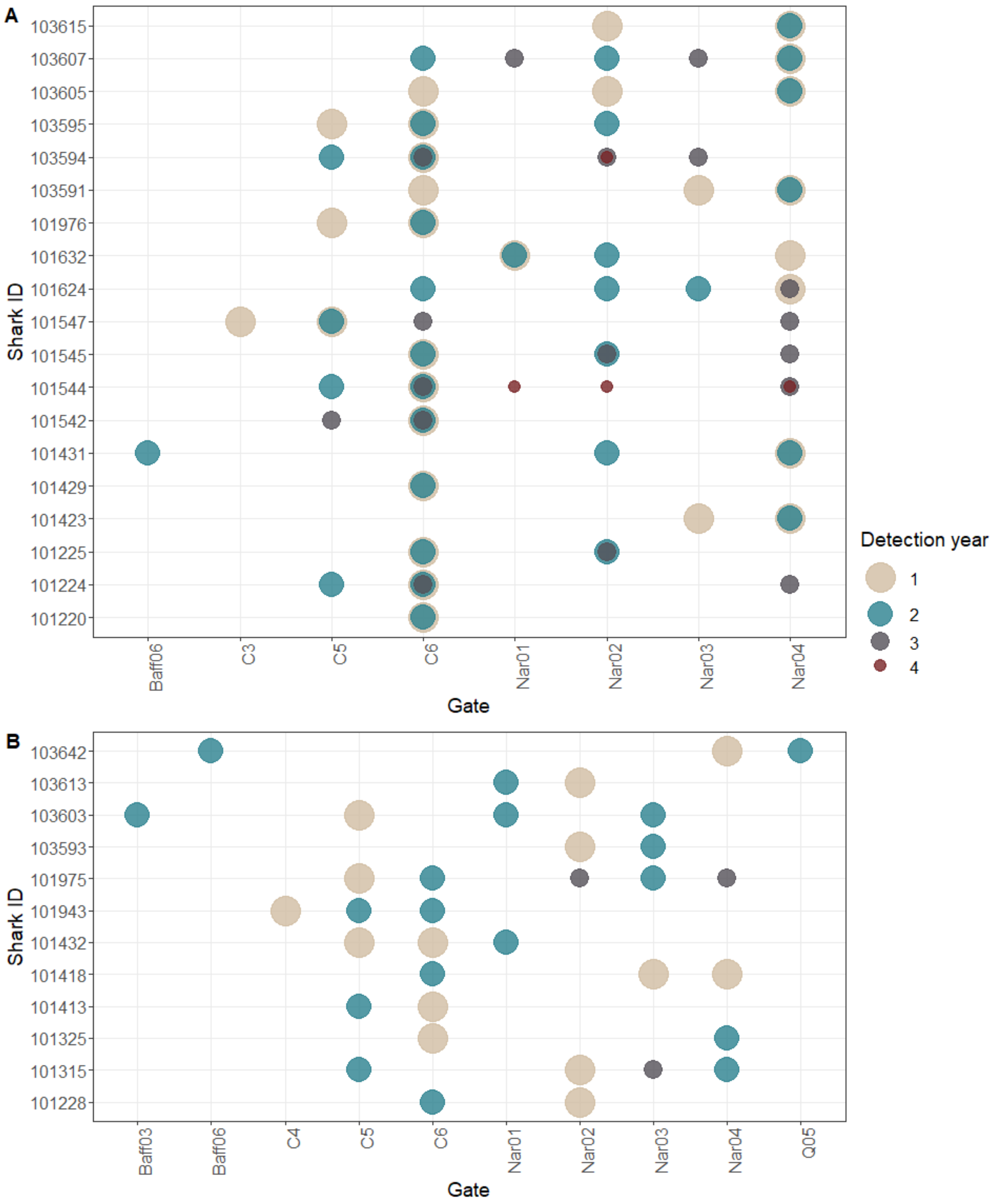

Figure 5.6 | Greenland shark detections recorded by acoustic receiver stations in offshore Baffin Bay (ABO, DST, and QIK arrays) across multiple study years, listed by the identification number of tagged sharks and by receiver gate. **A**) Sharks demonstrating spatial overlap in detection locations (*i.e.*, receiver gates) across years. **B**) sharks for which no spatial overlap across years was observed. Points are coloured by detection year for each individual, where year 1 represents the first year in which an individual was detected.

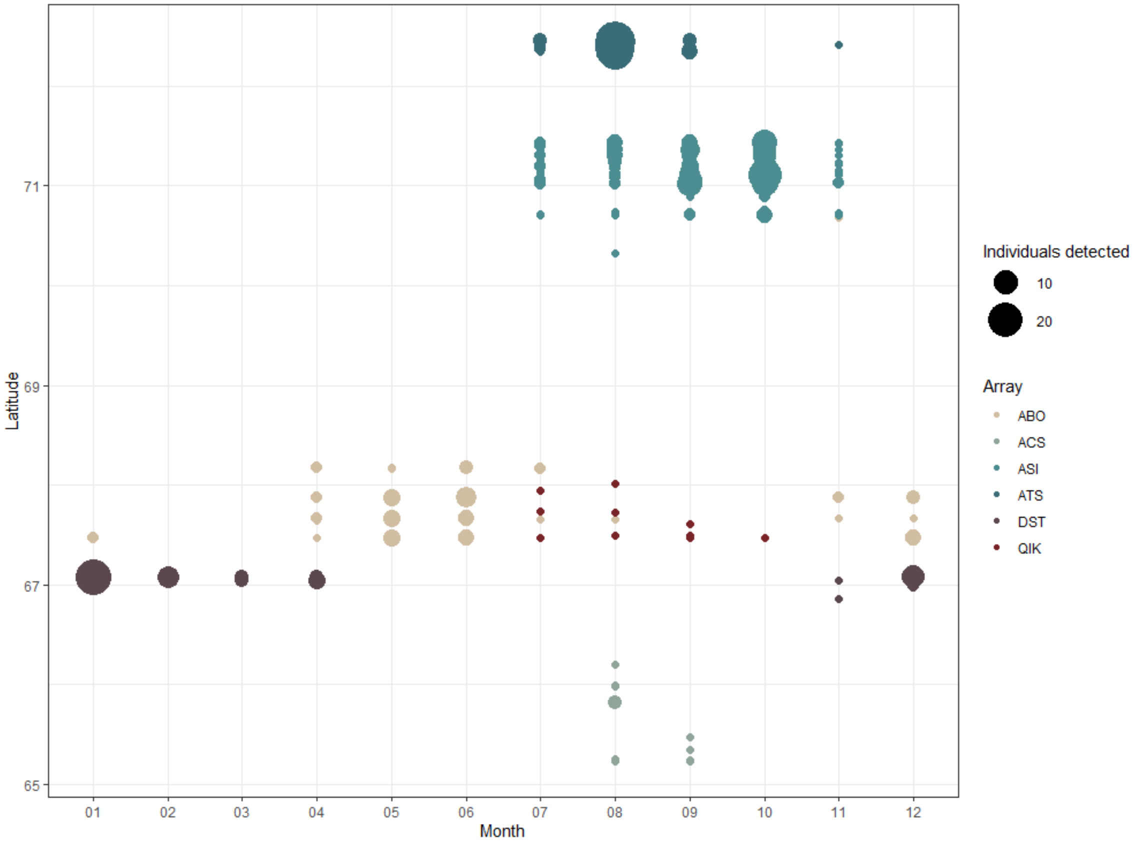

Figure 5.7 | Greenland shark detections arranged by month and latitude. Points are scaled by the number of unique individuals recorded at each time and location and are coloured by the array on which the detections were recorded. Array abbreviations are as follows: Arctic Baffin Offshore (ABO), Arctic Cumberland Sound (ACS), Arctic Scott Inlet (ASI), Arctic Tremblay Sound (ATS), Davis Strait (DST), Qikiqtarjuaq (QIK).

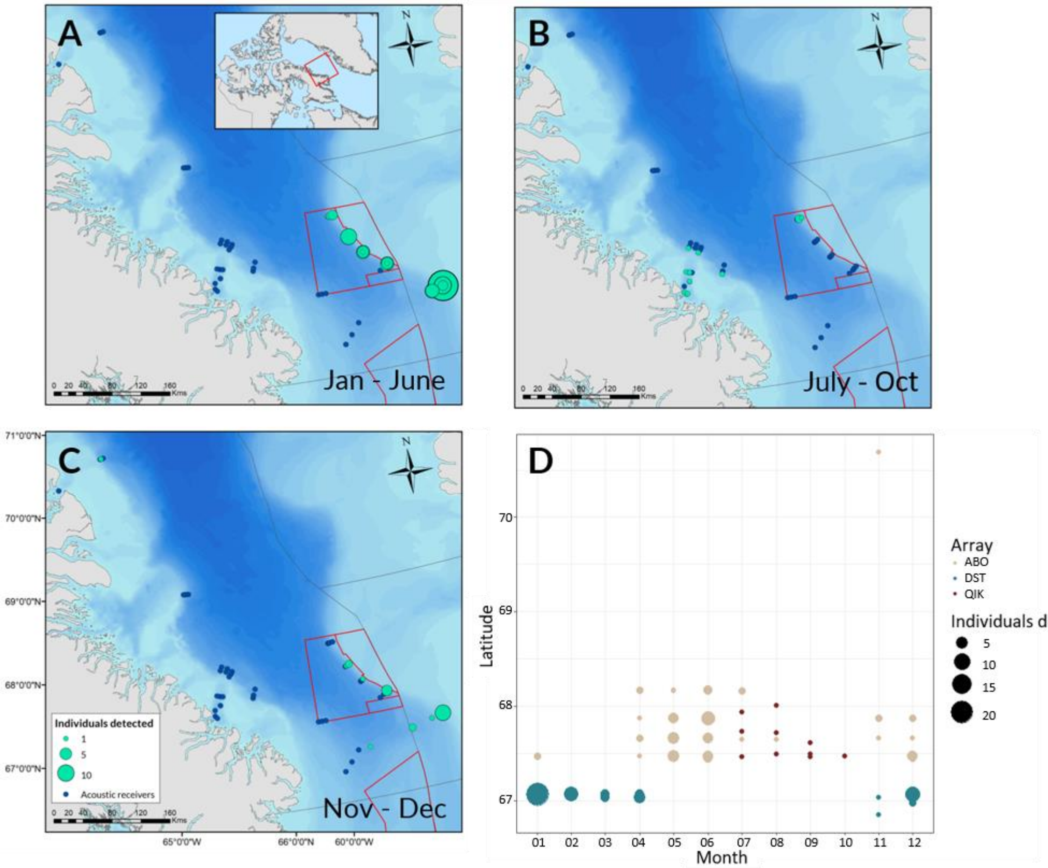

Figure 5.8 | Seasonality in coastal and offshore acoustic detections of Greenland sharks in southern Baffin Bay (NAFO subarea 0A). Panels A-C show detections recorded from Nov 2015 to Aug 2018 where points are scaled by the number of unique individuals recorded within each time period (January-June, July-October, and November-December) at each receiver location. Panel D shows detections from the same 3-year period grouped by month and latitude with points scaled by the number of individuals detected and coloured by array. Array abbreviations are as follows: Arctic Baffin Offshore (ABO), Davis Strait (DST), Qikiqtarjuaq (QIK).

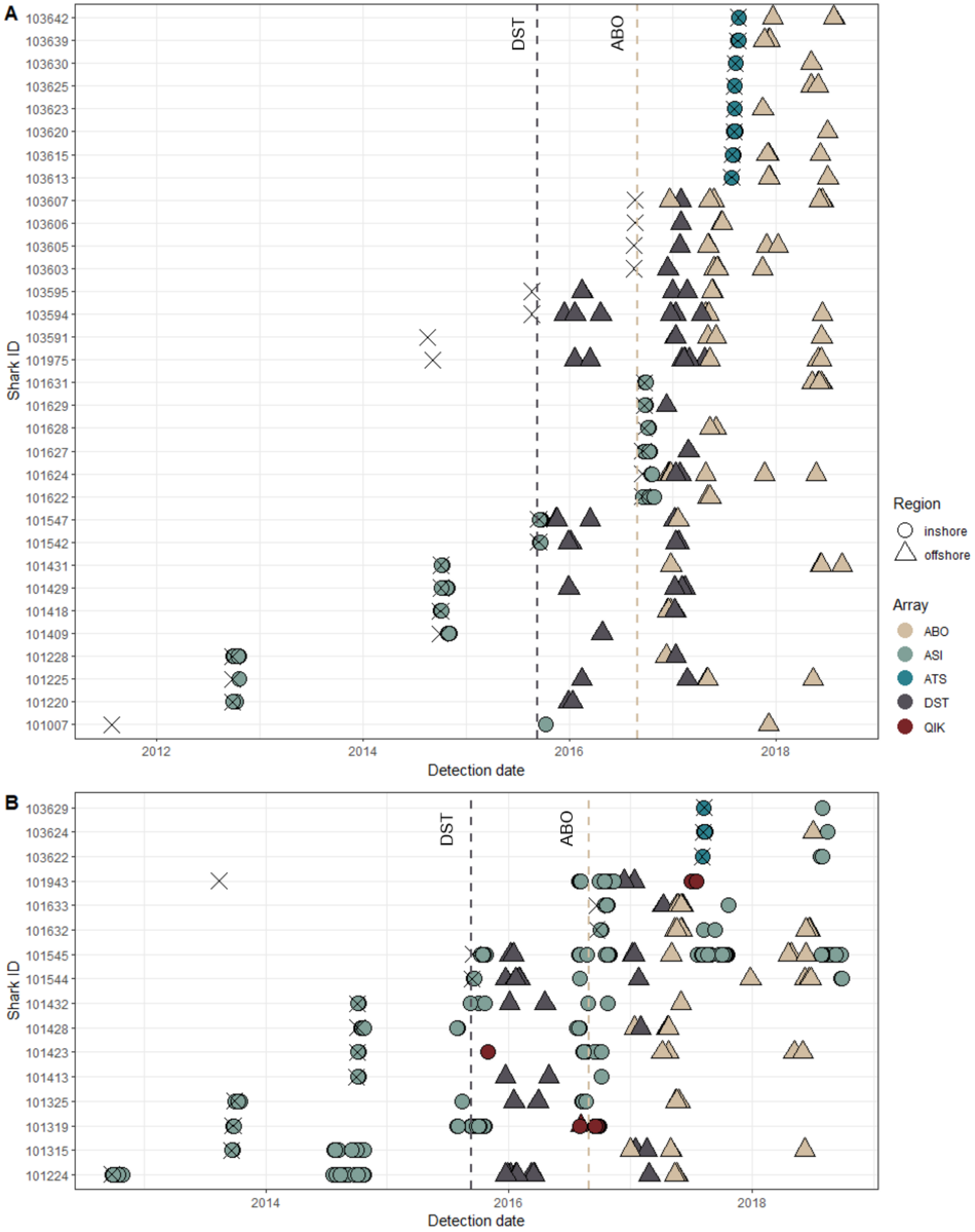

Figure 5.9 | Greenland shark detections recorded by acoustic receiver stations in multiple arrays in coastal and offshore Baffin Bay, listed by the identification number of tagged sharks and the time of detection. A) Sharks that were detected by more than one array but were detected in coastal waters in only one year. B) Sharks detected by more than one array and in coastal waters over multiple years. Point colour denotes the array on which detections were recorded and point shape indicates the location of the detection as either inshore or offshore. Dashed lines indicate the deployment date of arrays by corresponding colour. The date of tagging and release for each animal is marked by an ‘X’.

Table 5.1 | Summary data for 6 acoustic receiver arrays in the Arctic-OTN array network. Array names are abbreviated as follows: *ABO* = Baffin Offshore, *ACS* = Cumberland Sound, *ASI* = Scott Inlet, *ATS* = Tremblay Sound, *DST* = Davis Strait, and *QIK* = Qikiqtarjuaq. Marine region is listed as either inshore, offshore, or inshore & offshore depending on the location of moorings within each array. First deployment date refers to the initial deployment of receivers in the array, while last retrieval date refers to the most recent date on which data was collected from its receivers within the study period. The number of unique stations within each array are listed as the total number or as the mean and standard deviation of the number of stations deployed per year across all active years. Mean yearly detections are shown with standard deviation and the number of unique individuals detected by stations within each array are listed as the total number recorded over the entire study period.

Array name	**Marine region**	**First deployment**	**Last retrieval**	**Minimum latitude**	**Maximum latitude**	**Mean yearly stations**	**Yearly stations (range)**	**Mean yearly detections**	**Yearly detections (range)**	**Individuals detected**
ACS	Inshore	2010-08-16	2016-08-30	64.7679	66.3119	29 ± 19.3	15 - 56	325*	325*	8*
ASI	Inshore	2012-09-24	2018-10-08	70.3240	71.4394	68 ± 20.8	24 - 80	2,612 ± 1,684	812 - 5,308	85
ATS	Inshore	2017-03-23	2018-09-10	72.0542	72.7386	39 ± 5.66	35 - 43	16,523 ± 15,088	5,854 – 27,192	48
QIK	Inshore & offshore	2015-10-07	2018-09-26	67.4652	68.0687	7 ± 1.41 (inshore), 7.25 ± 1.26 (offshore)	13 - 17	24 ± 31.6	1 - 69	4
DST	Offshore	2015-09-09	2018-01-01	66.6413	67.2630	11	11	585 ± 306	232 - 786	34
ABO	Offshore	2016-08-31	2018-10-04	61.0000	72.0422	34 ± 0.58	34 - 35	477 ± 381	140 - 890	41

* Note that for the ACS array, only one year of detection data were available (2011), during which 56 receiver stations were actively deployed.

Table 5.2 | Mean duration, standard deviation, and range of Greenland shark detection events (hours and seconds) recorded by receiver gates in offshore Baffin Bay and listed in descending order based on mean event duration. Standard deviation is listed as NA where only single detection events were recorded. Total detection events and total detections refer to total values associated with all receivers in each gate, as recorded throughout the entire study period.

Gate	Mean event duration (h)	Mean event duration (sec)	SD (sec)	Range (sec)	Total detection events	Total detections
Nar04	18.19	65,469	182,617.67	0-798,900	40	931
Nar02	9.32	33,548.28	86,356.65	0-347,880	29	359
C6	8.46	30,473.46	87,040.39	0-476,880	55	1,260
Nar03	3.47	12,477.14	28,613.17	0-101,760	21	404
Nar01	3.28	11,813.33	37,193.66	0-160,080	18	162
C5	2.46	8,851.58	10,050.08	0-35,880	19	454
Baff06	2.20	7,920	8,909.55	1620-14,220	1	39
C4	0.80	2,880	593.97	2,460-3,300	2	33
C3	0.48	1,740	NA	1,740	1	7
Baff03	0	0	NA	0	1	1
Q02	0	0	NA	0	1	1
Q05	0	0	NA	0	1	1

CHAPTER 6
General Discussion

6.1 Summary

The Greenland shark is mobile, long-lived species that inhabits remote and seasonally-inaccessible regions of the Arctic and North Atlantic Oceans and can occupy depths of nearly 2,000 m (Campana, Fisk, & Peter Klimley, 2015). Despite the frequent incidental capture of Greenland sharks by commercial Arctic fisheries (Bryk, Hedges, & Treble, 2018), a persistent lack of knowledge of key biological traits and life history characteristics have limited efforts to develop and implement a species-specific management strategy (Davis et al., 2013; Edwards et al., 2019b). To address this issue, this thesis includes a complete summary of Greenland shark research conducted to date, which allowed the identification of research priorities and management strategies that could help to prevent future declines in Greenland shark populations (Edwards et al., 2019b). An additional summary of research tools, methodologies, and findings published in deep-water telemetry studies to date provided insight into the use of acoustic telemetry in the deep sea, informing my two subsequent data chapters. The final two chapters in this thesis defined the movement behaviours and habitat use of this understudied Arctic predator over a period of up to 7 years. These research findings improve our understanding of the Greenland shark's capacity to provide stability to Artic marine ecosystems by connecting coastal and offshore food webs. This work will also aid future assessments of the species' vulnerability to incidental capture by fisheries and other projected climate-induced environmental and anthropogenic threats.

Given growing concern over the vulnerability of Greenland sharks to threats posed by overexploitation and climate change (NAFO, 2017), a major objective of this thesis was to identify the knowledge gaps and research priorities that are critical to the development of a management plan for Greenland sharks and for long-lived species in general. By consulting and collaborating with Greenland shark experts from both research and management sectors, and using their previously published research as a guide, I identified eight key research topics which were deemed of the highest priority for future research and management (Edwards et al., 2019b). In the context of this thesis, the subsection focusing on Greenland shark movement ecology (*section 2.6*) identified the use of static acoustic telemetry and long-lifespan transmitters as a viable approach for examining the long-term movements of Greenland sharks at various spatial scales. Furthermore, the suggested use of acoustic detection data and environmental records to identify drivers of Greenland shark movement was crucial for directing subsequent work conducted in Chapter 4 of this thesis. Overall, this chapter provides an updated summary of our current knowledge of Greenland shark biology, physiology, and ecology, while placing it in the context of conservation and management by identifying future research priorities, potential strategies, and management tools.

In Chapter 3, I presented a synthesis of telemetry studies conducted in the deep sea (>200 m depth) to date, including movement records spanning from the surface down to 5,900 m depth for species from 13 deep-water families (Edwards, Pratt, Tress, & Hussey, 2019). Importantly, this review highlighted a number of considerations relevant to the study of Greenland sharks, including specific tagging and release methods developed for deep-water species which aim to minimize physical stress and reduce mortality rates (*e.g.*, reducing haul speed for capture via longlines). This research also provided evidence that, despite the 500 m depth rating of commercially-available acoustic receivers (VEMCO product specifications, https://vemco.com), several studies have successfully deployed receivers at depths exceeding this limit, generating movement records of unprecedented durations for two deep-water species (Barkley, Hussey, Fisk, Hedges, & Treble, 2018; Daley, Williams, Green, Barker, & Brodie, 2015; Hussey et al., 2017). The exemplary research methodologies, analyses, and findings presented in this chapter, in addition to the technological innovations proposed, provide a comprehensive guide for advancing research on the movement ecology of deep-sea organisms.

Using many of the telemetry techniques outlined in Chapter 3, 6 years of archived acoustic detections allowed an examination of the long-term residency and movement behaviours of 65 tagged Greenland sharks in a model deep-water Arctic fjord (Scott Inlet, Nunavut) (see Chapter 4). This chapter identified sea-ice cover as a strong predictor of Greenland shark presence in the fjord (verified using a GLMM) and described the seasonal timing of Greenland shark residency as the summer ice-free period between July and October. Juvenile sharks were found to have a longer duration of residency that subadults, however, both age-classes showed activity in similar regions of the fjord and used the same proportion of the fjord's total area. Sharks also exited the fjord at approximately the same time during both tagging and return years, however, the detection profiles of sharks that returned to the fjord in subsequent years illustrated that sharks arrive in coastal waters much earlier than when tagging efforts are typically conducted. Lastly, the system's main deep-water channel was identified as an important corridor for transitional movements between offshore waters and coastal systems, where bathymetric features such as channel banks may provide a navigational cue to guide shark movements.

To expand upon the fine-scale analyses conducted in Chapter 4, Chapter 5 presented a broad-scale examination of the movements of 155 tagged Greenland sharks across 4 coastal systems and the offshore waters of Baffin Bay. Similar to Chapter 4, these results demonstrated a strong seasonal pattern in the use of coastal and offshore environments by tagged sharks. Specifically, detections in coastal habitats were recorded strictly during the ice-free summer period between July and November (with an overlap in habitat use observed during these two months), while offshore detections were recorded across the remaining winter months, with fewer detections reported in July and August and an absence of offshore detections during September and October. The majority of offshore detections were recorded by receivers in the southeastern region of Baffin Bay in the vicinity of a fishery closure (DFO, 2008b), however, there was a notable lack of detections along the basin’s western continental slope. Over half of the tagged sharks detected in the offshore were redetected for up to a maximum of 4 years, during which many individuals revisited the locations of receivers by which they were detected in previous years. Many sharks were also detected by receivers across multiple coastal and offshore receiver arrays, demonstrating a high degree of connectivity throughout the study system.

6.2 Implications

Arctic ecosystems experience dramatic seasonal fluctuations in solar radiation, resulting in dynamic fluctuations in sea ice cover, and consequently, the degree of ice-associated and pelagic primary production which form the base of Arctic marine food webs (Gradinger, 1995; J. E. Walsh, 2008). Mobile Arctic species have adapted to these predictable shifts by adopting movement patterns that correspond to the occurrence of desirable environmental conditions, for instance, by moving between seasonally available regions of high productivity (Barkley et al., 2018; Dueck, Hiede-Jørgensen, Jensen, & Postma, 2007; K. L. Laidre et al., 2004; Marcoux, Ferguson, Roy, Bedard, & Simard, 2017). However, with polar regions warming at an unprecedented rate (ACIA, 2005), the predictability of environmental fluctuations may be reduced, which could have catastrophic impacts on long-lived or otherwise slow-adapting species. This is especially concerning for Arctic marine megafauna (*i.e.*, teleost fishes, elasmobranchs, and marine mammals), which includes many species that rely on ice-derived primary production (Fossheim et al., 2015) or that use sea-ice for essential behaviours (Laidre et al., 2015; Tynan & Demaster, 2016; Wassmann, Duarte, Agustí, & Sejr, 2011). Arctic ecosystems also contain a large number of understudied species - marine fishes in particular - for which very little baseline biological and ecological research has been conducted (Dey, Yurkowski, Schuster, Shiffman, & Bittick, 2018). Given the predicted northward expansion of commercial fisheries and other human activities (Christiansen, Mecklenburg, & Karamushko, 2014; Huntington et al., 2007), these data are invaluable to ensuring the conservation of Arctic biodiversity.

Deep sea ecosystems face a similar predicament, where the rate of new research discoveries is currently exceeded by the rate of innovation in resource exploitation, leading to shifts in baseline ecological conditions prior to the appearance of their full descriptions in the published scientific literature (Edwards et al., 2019a). Additionally, despite the vast distance separating the deep sea from the atmospheric and climatic changes observed at the surface and on land, the majority of deep-water food webs rely on nutrients originating from terrestrial sources and the photic zone and are therefore highly dependent on the state of these environments (Armstrong, Foley, Tinch, & van den Hove, 2012; Smith, Priede, Bagley, & Addison, 1997). In the Arctic, the composition and abundance of primary productivity is being influenced by climate-induced changes to sea surface temperatures, salinity (due to increased terrestrial fresh-water runoff), and sea-ice cover (Duarte et al., 2012; Li, McLaughlin, Lovejoy, & Carmack, 2009; Wassmann et al., 2011). It is therefore likely that while the exploitation of Arctic deep-water species increases (due to reductions in sea ice which will allow a greater number of fishing vessels access to polar waters (Christiansen et al., 2014)), the loss of ice-derived primary productivity will simultaneously result in significant impacts on the same deep-water ecosystems and demersal species being targeted.

This thesis presents novel data that addresses some of the major knowledge gaps identified for a key Arctic top predator (Edwards et al., 2019b) and provides support for its potential importance in providing stability to Artic marine ecosystems (McCann, Rasmussen, & Umbanhowar, 2005). Specifically, the telemetry analyses conducted in Chapters 4 and 5 addressed two major areas of concern relating to the management of Greenland sharks via the study of their movement ecology. These included the previous lack of long-term (multi-year) movement records, that prevented the detection of seasonal movement patterns and limited our knowledge of the Greenland shark’s distribution and its capacity for long-range movement (Edwards et al., 2019b). Results from both chapters illustrated a seasonal pattern in the use of two Arctic habitat types (coastal fjords and offshore waters) which provides an indication of behavioural flexibility exhibited by this species. This finding also has important implications for fisheries management and could aid in the implementation of spatial management strategies such as timed regional closures and Dynamic Area Management (Edwards et al., 2019b). Furthermore, the importance of sea ice for predicting the presence of Greenland sharks in coastal systems (Chapter 4) suggests that the predictability of these seasonal movements may be altered by the loss of this environmental cue, implying that continued monitoring will be essential as the Arctic climate continues to change.

My results also demonstrated a high degree of connectivity among habitats across Baffin Bay and eastern Baffin Island (Chapter 5). This fact, along with their observed response to seasonal environmental shifts, suggests that Greenland sharks likely play a role in both coastal and pelagic food webs, and may therefore help to confer community stability (McCann et al., 2005). In addition, these results indicate that individual home ranges may extend across an entire ocean basin, implying that this species will likely require multi-national agreements for effective management at the population level (Edwards et al., 2019b).

Finally, many of the considerations proposed in Chapter 2 may be more broadly applied to the management of other long-lived organisms, including many Arctic and deep-water species. In particular, it is essential for the duration of monitoring to reflect the temporal scale of the examined movement behaviours, particularly for species whose movements may extend over vast distances or whose movement patterns occur over long durations (Edwards et al., 2019a). As such, collaboration among researchers, stakeholders, and management institutions is highly recommended to improve the management of deep-water fisheries and the conservation of vulnerable long-lived species.

6.3 Future directions

While the results presented in this thesis have filled some of the knowledge gaps relevant to the study of Greenland sharks, many more questions have yet to be addressed, including some that were inspired by my own research findings.

Firstly, the effective management of Greenland sharks will require further research and technological innovations to determine key biological traits such as generation times and fecundity, and to facilitate the collection of demographic data including population sizes, the extent of their geographic range, and the locations of mating grounds (Edwards et al., 2019b).

There is also much work to be done in the field of Greenland shark movement ecology. For example, future telemetry studies would benefit from additional research into the fine-scale movement behaviours of Greenland sharks (swim speed, track tortuosity, etc.) in both coastal and offshore environments. This insight would guide the development of acoustic arrays designed to maximize detection efficiency and to capture important movement behaviours exhibited in a variety of habitat types. Additional studies should also address the question of how fine-scale horizontal movements exhibited after tagging and release may be affected by capture-induced stress. This would provide further confidence in the reliability of movements recorded during the post-tagging period and could reveal the amount of time required for tagged individuals to return to natural movement behaviours following release. Arrays that incorporate fine-scale positioning technologies, for example the VEMCO positioning system (VPS; VEMCO, Bedford, NS, Canada), or the use of multiple timed-release satellite tags on individual Greenland sharks (Hussey et al., 2018) provide two commercially available options for obtaining such data.

Perhaps the most obvious question arising from this research relates to a discrepancy between the timing of Greenland shark presence in coastal waters reported in this thesis, and the timing of previous shark encounters cited by scientific reports and in the published literature. Despite a consistent lack of winter detections recorded by coastal receiver arrays in this study, reports from both commercial and scientific fisheries provide evidence of the presence of Greenland sharks in coastal systems during the winter ice-covered period (DFO, 2008a; Treble & Stewart, 2010; P. Walsh, 2018; Wheeland & Devine, 2018). This inconsistency suggests that the full range of behaviours exhibited by the sampled population are not demonstrated by the individuals tagged in this study. This presents a significant problem, as our results, if taken on their own, would inaccurately suggest that Greenland sharks in Baffin Bay are safe from capture by winter fisheries conducted through the sea-ice in coastal regions. While conducting Arctic fieldwork during the winter is impeded by a number of logistical challenges, I propose that by tagging Greenland sharks captured through the ice in coastal waters, we might reveal an additional behavioural archetype not demonstrated by individuals in the current study. In addition, by comparing movement records to a wider range of potential drivers (*e.g.*, dissolved oxygen, primary production, or prey availability), an explanation for this apparent dichotomy could be revealed. This work would have broader implications for the management of commercial and community-based fisheries in the region and could shed light on behavioural variability exhibited by this enigmatic species.

In conclusion, acoustic telemetry provides a valuable tool for understanding the movement behaviours of animals that inhabit obscure or inaccessible habitats. Long-lived species, such as those found in deep-water Arctic environments, often possess biological traits which make them susceptible to population declines (Edwards et al., 2019b). As such, further adaptation of telemetry technologies and approaches for use in these environments will be invaluable for defining population ranges, improving stock assessments, and allowing the delineation of biologically relevant spatial management approaches. By dedicating additional time and effort to this research, we might ultimately prevent the loss of long-lived species such as the Greenland shark and can ensure the longevity and future stability of these fragile ecosystems.

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