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Reproduction, distribution, and feeding ecology of the Greenland shark (*Sominosus microcephalus*) in relation to climate change and human activities in the Arctic

The Greenland shark (*Sominosus microcephalus*) is one of multiple sleeper shark species, but due to its habitat preferences, the Greenland shark is one of the least studied vertebrates in the Arctic ocean. The distribution of this shark, both geographically and within the water column, along with feeding habits and reproduction strategies are examined below in an effort to provide an analytical synthesis of available research. Scientific research studies, as well as traditional ecological knowledge of the Greenland shark, contribute to a discussion of how this species may be impacted by climate change and increasing human activity in the Arctic ocean and surrounding waters. Without population estimates of this species, it is impossible to estimate the damage of fishing industries and decreasing sea ice extent.

Introduction

The Greenland shark (*Sominosus microcephalus*) is one of the least studied Arctic marine vertebrates and is categorized by the Norwegian Red List as "Data Deficient" (Neilsen *et al.* 2018). Very little research and Inuit records exist on the Greenland shark due to its lack of commercial interest and limited importance to Inuit diet (Idrobo and Berkes 2012). A significant amount of data on distribution, abundance, and diet derives from Greenland fisheries and Inuit hunters in Greenland, as well as recent research studies by Arctic scientists. The Arctic population of the Greenland shark inhabits arctic waters ranging between the West coast of Greenland, the Northern coast of Russia, and the North-eastern coast of Canada (Yano *et al.* 2007). This shark is the largest marine vertebrate in the Arctic region, reaching sizes upwards of 756 centimeters, but on average they are 300 to 500 centimeters long (Nielsen *et al.* 2016). Typically, females have been found to grow significantly larger than males (Yano *et al.* 2007). Most likely due to their size and habitat, Greenland sharks are thought to be slow swimming predators compared to sharks of comparable size (Nielsen *et al.* 2016). This species was thought to be a benthic-feeding organism relying on prey such as halibut, skates, crabs, squid, and snails, but Greenland sharks have been documented utilizing the entire water column for feeding (Yano *et al.* 2007; MacNeil *et al.* 2012). In recent years, studies have shown that Greenland sharks can feed in pelagic zones of the Arctic and stomach content analyses have shown pinnipeds, such as ringed and harp seals (*Phoca hispida & Phoca groenlandica*), Atlantic salmon (*Salmo salar*), cod, beluga (*Delphinapterus leucas*), and walrus (*Odobenus* rosmarus) are within the sharks' diet (MacNeil *et al.* 2012). Although some of these prey species are thought to have been scavenged, Inuit hunters have observed Greenland shark bite wounds on ringed seals proving evidence that direct attack can also occur (Idrobo and Berkes 2012). Little is known about the annual timing of reproduction for Greenland sharks, but researchers estimate shark pups are born between July and August and are between 40 and 100 centimeters in length when born (Hussey *et al.* 2014; Yano *et al.* 2007). Although preferred breeding and pupping grounds lack significant research, it is believed that female Greenland sharks prefer fjord habitats for pupping (Hussey *et al.* 2014; Hussey *et al.* 2018). The unique life history, distribution, and feeding ecology of the Greenland shark cause this species to be at a significantly higher risk for exploitation and population decline within Arctic regions.

Distribution

The Greenland shark has a range spanning from the northernmost points in the Arctic Ocean down to the eastern coast of the United States (Yano *et al.* 2007, see fig. 2). Given their preference for extremely cold temperatures, the Greenland shark could potentially have a range much larger than scientist believe. The Arctic population of Greenland shark is known to mostly inhabit the waters around the west coast of Greenland, the northeastern coast of Canada and the north-western coast of Russia (Chernova *et al.* 2015). Due to the prevalence of Greenland halibut fisheries, most documented catches and sightings have been reported as bycatch on long-lines and gillnets near Baffin Bay as well as the Labrador Basin (Neilsen *et al.* 2014; Yano *et al.* 2007). Scientists have utilized these fisheries' bycatch data in order to estimate a geographical range, as well as areas where abundance is higher. In a 2014 study by Nielsen et. al, they found that 106 Greenland sharks were caught between 59.5°N and 74.6°N off the west coast of Greenland and in a similar latitude on the west coast of Greenland (Nielsen *et al.* 2014). Most sharks were caught near the continental shelf break to the south and in deeper bays to the north (Neilsen *et al.* 2014). Given this data, as well as Yano et al.'s findings from 2007 correlating more sharks at higher latitudes, it can be deducted that Greenland sharks prefer higher latitudes where various water depths exist.

In a more recent study, Chernova et al. noted the first recorded sighting of a Greenland shark in the Laptev Sea north of Russia, which is the easternmost record of this species (Chernova *et al.* 2015). Due to the lack of commercial fishing and reported bycatch in this area, Greenland sharks were previously unknown to inhabit Arctic waters eastward of the Barents Sea (Chernova *et al.* 2015). The preferred water temperature of this species is between 0 and 6°C, and the Laptev Sea to the north contains this preferred habitat due to the West-Spitsbergen Current coming from the Atlantic Ocean (Campana *et al.* 2013; Chernova *et al.* 2015). Although this may be a rare occurrence, this data shows that Greenland sharks may follow these cold, deep-water currents to various regions across both Arctic and Atlantic waters. Scientists have yet to truly understand just how large the Greenland sharks' geographically range is definitively, but it is possible that these sharks could survive anywhere in the global oceans if the temperature is cold enough.

Tagged Greenland sharks have been tracked following certain migration routes along the north-western coast of the Canadian Arctic and the Western coast of Greenland (Hussey *et al.* 2018). This data has led to a hypothesis that this species may undergo a seasonal migration from shallower waters, into the open waters of Baffin Bay, and then into coastal fjords along western Greenland (Hussey *et al.* 2018; see fig. 1). Within these coastal fjords of Greenland, sharks found were mostly mature females, and 42.3% were juveniles less than 200 centimeters long (Hussey *et. al.* 2014). It can be deducted that female Greenland sharks use these shallower regions as birthing grounds (Hussey *et al.* 2014), as they could provide safety from marine predators of juvenile sharks. Juvenile sharks were more commonly found between July to September (Hussey *et al.* 2014), so annual migration most likely occurs during spring months. This migration pattern would correlate with the timing of not only the sea ice breakup, but seal births as well (Stroeve *et al.* 2012; Ferguson *et al.* 2005). Mature Greenland sharks could feed while migrating under the sea ice on ice seals as well as seal pups because most seals give birth on sea ice between April and May (Ferguson *et al.* 2005). As the sea ice breaks up in June (Stoeve *et al.* 2012), the coastal fjord regions would contain less ice cover and could provide adequate birthing grounds for the Greenland shark July through September.

Within the water column, Greenland sharks undergo large vertical migrations. Greenland sharks have been observed at depths ranging from less than one meter deep to over 1,200 meters deep

(MacNeil *et al.* 2012), demonstrating that this species can survive at most oceanic depths. In a 2004 study by Skomal and Benz, they tagged six Greenland sharks over the course of 31.1 to 48 hours and found a clear pattern of daily vertical migration (Skomal and Benz 2012). Between 10 P.M. and 3 A.M., Greenland sharks ascended to shallower depths of less than 100 meters and during daylight hours, sharks descended rapidly to depths of 200 meters or more (Skomal and Benz 2012). This data points to a potential nocturnal feeding pattern at shallower depths and benthic feeding during the day due to prey availability. The depth at which Greenland sharks commonly inhabit also correlates with size, and therefore age, as found in a 2007 study by Yano et al. and a 2014 study by Nielsen et al. (Yano *et al.* 2007; Nielsen *et al.* 2014). The depth of capture for all sharks ranged from less than 100 meters to over 1,248 meters deep (Nielsen *et al.* 2014). Sharks less than 150 centimeters in length were caught at depths shallower than 900 meters (Nielsen *et al.* 2014), indicating a preference for smaller sharks to remain closer to the pelagic zone. Sharks ranging from 200 to 300 centimeters were caught between 250 to 1,050 meters and sharks greater than 300 centimeters were most frequently caught deeper than 1,000 meters (Yano *et al.* 2007). This data indicates that larger and older sharks are more frequently inhabiting the benthic zones of the water column. While there have been no proposed hypotheses to date regarding why this size and depth correlation may occur, it could be related to a physiological factor preventing smaller sharks from diving to greater depths for long periods of time.

Feeding

Greenland sharks were historically believed to be benthic feeders, but recent studies and stomach content analyses have found a diverse range of species within the Greenland sharks' diet. One of the most important components of the Greenland sharks' prey is fish, including over 25 different species (Yano *et al.* 2007). Benthic feeding fish, such as the Greenland halibut (*Reinhardtius hippoglossoides*), were found to compose a majority of the Greenland sharks' diet and were present in 67.57% of Greenland shark stomachs analyzed (Yano *et al.* 2007). Another benthic fish species commonly found was beaked redfish (*Sebastes mentella*) and was present in 21.6% of all shark stomachs analyzed (Yano *et al.* 2007). To researchers' surprise, benthic species only accounted for a little over half of all prey species found within the Greenland sharks (Yano *et al.* 2007, see fig 2). Atlantic salmon (*Salmo salar*), herring (*Clupea harengus*), and capelin

(*Mallotus villosus*) have also been abundantly present in Greenland sharks' stomachs (MacNeil *et al.* 2012), which contradicts prior belief that this species primarily feeds on benthic organisms.

As benthic and pelagic carnivores, the Greenland shark also actively feeds on larger marine animals such as ringed seal (*Phoca hispida*), hooded seal (*Crystophora cristata*), bearded seal (*Erignathus barbatus*), and harp seal (*Phoca groenlandica*) (Yano *et al.* 2007; MacNeil *et al.* 2012). Pinnipeds make up a significant portion of the Greenland sharks diet, and were found in 16.22% of Greenland shark stomachs analyzed (Yano *et al.* 2007). Compared to Arctic fishes, Arctic seals have an a much larger fat content ranging between 20 and 60% of body mass (Aarseth *et al.* 1999). Predation on Arctic seals would provide Greenland sharks with a much larger fat intake, and therefore would be worth the energy expenditure associated with preying on pinnipeds. Although observational feeding of the Greenland shark on pinnipeds has yet to be documented, researchers assume that these species are actively caught rather than scavenged upon (Macneil *et al.* 2012). According to Canadian Inuit hunters, whole seal pups have been found within Greenland shark stomachs leading to the assumption that these pups have been actively preyed upon through holes within seal dens (Idrobo and Berkes 2012).

Greenland sharks are typically blind and generally slow swimming fish, but certain adaptations help them to be successful predators of Arctic waters (Macneil *et al.* 2012). Greenland sharks do not biologically have poor eyesight, but a vast majority are infected by a parasitic copepod called *Ommatokoita elongata* (MacNeil *et al.* 2012, see fig. 4). This parasite attaches to the sharks' cornea and causes partial or total blindness, usually in both eyes (MacNeil *et al.* 2012). Out of 1,505 Greenland sharks analyzed from East Greenland, 98.9% were infected in both eyes by *O. elongata* (Berland *et al.* 1961) and out of six sharks analyzed near Baffin Island, 100% carried *O. elongata* (Skomal and Benz 2004). Even when the parasite dies or leaves the individual Greenland shark as a host, scars and lesions are left behind that greatly impair vision (MacNeil *et al.* 2012). This prevalence of this parasite that induces blindness has led researchers to believe that the Greenland shark relies on other specialized adaptations to find prey (MacNeil *et al.* 2012). A heightened sense of olfaction could allow the Greenland shark to rely heavily on smell rather than eyesight in order to track and find prey along the bottom of the ocean floor, as well as in pelagic zones near the surface (MacNeil *et al.* 2012; Idrobo and Berkes 2012). Another theory presented by Skomal and Benz is that the Greenland shark may depend heavily on electroreception in order to detect electrical fields generated by targeted prey (Skomal and Benz 2004). An increased sense of olfaction as well as electroreception are adaptations that most species of sharks around the world utilize (Kimber *et al.* 2014), and the Greenland shark is no exception. These adaptations could make up for a lack of eyesight and could be instrumental in the Greenland sharks' ability to successfully find and capture prey.

Although typically the Greenland shark cruises slowly at deep oceanic depths, they have been recorded making rapid ascents and descents within the water column (Skomal and Benz 2004). Due to the extremely cold temperatures the Greenland shark inhabits and their large body size, swimming slowly may conserve vital energy needed to capture prey. On average, the Greenland shark swims at about 0.06 m s^{-1} along the ocean floor (Skomal and Benz 2004). During ascent and descent, Greenland sharks were recorded reaching speeds of over 0.5 m s^{-1} (Skomal and Benz 2004). Although ascent rates were somewhat lower than descent rates (Skomal and Benz 2004), this data shows that the Greenland shark is capable of short bursts of fast speeds if necessary. The capacity to reach faster speeds is most likely a key factor in the Greenland sharks' ability to catch faster moving prey such as Arctic cod (*Boreogadus saida*) and species of pinniped.

Within the Arctic food web, the Greenland shark plays an important role not only as a benthic feeder, but as a scavenger and an apex predator as well. The Greenland shark primarily relies on live prey to feed on, but in many cases, they have been documented scavenging on larger prey such as whales and walrus. In a 2011 study by Leclerc et al., researchers discovered minke whale blubber (*Balaenoptera acutrostrata*) within the intestines of Greenland sharks off of Svalbard, Norway (Leclerc *et al.* 2011). Using genetic markers from whales that had been killed during Norwegian whaling expeditions, researchers were able to conclude that the blubber eaten matched the whales that had been hunted by whalers (Leclerc *et al.* 2011). This proved that the Greenland shark actively scavenges off of recently deceased marine vertebrates. Other prey such as porpoises, walrus, jellyfish, and crabs have all been identified in stomach content analyses of the Greenland shark (MacNeil *et al.* 2012), which demonstrates the opportunistic feeding pattern of this species. This opportunistic prey selection is also reflected by different prey preferences in different regions. For example, Greenland shark caught off of Iceland had a higher percentage of blue ling (*Molva Dyptergia*) and beaked red fish compared to Greenland shark caught off of

Western Greenland (McMeans *et al.* 2010). Overall, the Greenland shark is an opportunistic scavenger as well as an apex predator within Arctic waters.

Reproduction

Greenland sharks grow significantly slowly over the course of hundreds of years, and most female sharks don't reach sexual maturity until over 100 years old (Nielsen *et al.* 2018). Using isotope measurements from Greenland shark eye lens' nuclei, Nielsen and colleagues were able to age 28 female Greenland sharks within a few decades of accuracy (Neilsen *et al.* 2018). The two largest female sharks measured in at 493 and 502 centimeters and were aged to be 335 ± 75 and 392 ± 120 years old, respectively (Neilsen *et al.* 2018). Given this data, it is apparent that female Greenland sharks mature at a much older age than vertebrates of similar size (Neilsen *et al.* 2018). Mature females are generally larger than 400 centimeters long, while males mature around 300 centimeters (Yano *et. al* 2007). According to Neilsen et al.'s study, this would make the age of sexual maturity to be around 156 years old for female Greenland sharks (Neilsen *et al.* 2018). Given that female Greenland sharks can be over 500 centimeters long, females have an average lifespan of over 272 years (Neilsen *et al.* 2018; Yano *et al.* 2007). Males grow to significantly smaller sizes than females, but no studies to date have determined the age at which male Greenland sharks sexually mature (Yano *et al.* 2007).

The reproductive organs of the Greenland shark increase in mass and width as the shark grows, and a clear trend can be identified between body length of the shark and the mass of ovaries, the width of the uterus, and the mass of testes (Yano *et al.* 2007). Female Greenland sharks can contain over 3,000 unfertilized eggs after reaching sexual maturity (MacNeil *et al.* 2012, see fig. 5), but the mass of the ovaries and the width of the uterus change dramatically over the course of a female shark's life (Yano *et al.* 2007). Between 100 centimeters long and 425 centimeters long, a female Greenland shark's uterus width changes from about 5mm to over 35 mm thick (Yano *et al.* 2007). This exponential change is mirrored in ovary mass as well; at 150 centimeters long ovary mass is approximately 200 grams, and at 450 centimeters long ovary mass is over 1,500 grams (Yano *et al.* 2007). Ovary mass increases exponentially as length of a female shark increases (Yano *et. al* 2007), which potentially means older and larger sharks can produce more offspring. Male Greenland sharks follow a similar trend as testes mass goes from less than 100 grams at 175 centimeters long, to almost 1,600 grams at 400 centimeters long (Yano *et al.* 2007).

This research provides evidence that the reproductive maturity of both female and male Greenland sharks occurs over an extended period of time (potentially hundreds of years) as sharks grow in length.

Female Greenland sharks produce a limited number of larger, yolk-dependent offspring during reproduction, which is similar to other K-selected species (MacNeil *et al.* 2012). Although it is unknown how frequently the Greenland shark reproduces, it can be hypothesized that the Greenland shark reproduces annually or biannually due to known migration routes followed each year (Hussey *et al.* 2018). Multiple juvenile Greenland sharks have been identified with remnants of the egg yolk still attached (MacNeil *et al.* 2012). These juveniles had an average length of 40 centimeters, and the presence of the egg-yolk led researchers to believe these sharks were a few days old or less (Yano *et al.* 2007). Although thousands of oocytes have been found within female Greenland sharks' ovaries, only a small fraction of oocytes are successfully fertilized and born (Yano *et al.* 2007). An average litter size is approximately 10 shark pups for a medium-length female shark (Yano *et al.* 2007). The Greenland sharks' small litter size, large pup size at birth, and relatively infrequent reproduction categorizes this species as a K-selected species similar to Arctic whales and seals.

Climate Change and Human Activity in the Arctic

Between the 16th and 20th centuries, the Greenland shark was heavily harvested by Arctic bordering countries for shark liver oil (Davis *et al.* 2013). The earliest record for targeted fishing began in the 14th century in Iceland, but the shark fishing industry reached its peak in 1948 (MacNeil *et al.* 2012). The demand for shark liver oil by European countries was so high that harvest increased from 1,200 individuals in 1868 to 58,000 individuals in 1948 (MacNeil *et al.* 2012). Greenland shark liver oil was exported by the hundreds of barrels (MacNeil *et al.* 2012), but the damage on shark populations remains unknown to this day due to a lack of population estimates (Davis *et al.* 2013). The demand for shark liver oil decreased exponentially during the latter half of the 1900's, and large scale commercial fishing for the Greenland shark stopped entirely by 1970 (Davis *et al.* 2013). This historical massive fishing industry of the Greenland shark poses an interesting question to researchers as population risks are actively assessed in the present.

Currently, the only targeted fishing of the Greenland shark occurs off of Iceland and Greenland for human and dog food. In both regions, Inuit and local communities hunt the Greenland shark, but no large-scale market for shark meat has been developed (MacNeil *et al.* 2012). In Iceland, the Greenland shark is used for a delicacy dish called *hakarl* and a directed fishery remains in place (MacNeil *et al.* 2012). In Greenland, the Greenland shark is primarily caught in order to produce dog food in local communities, but occasionally the skin is utilized for bookbinding and knives (MacNeil *et al.* 2012). Targeted fishing for the Greenland sharks remains limited to these two regions, as well as a few Inuit communities in the north-eastern Canadian arctic (Davis *et al.* 2012). Although direct fishing is currently extremely limited, the Greenland shark faces other numerous threats from human activity in the Arctic.

Bycatch of the Greenland shark by Arctic fisheries occurs frequently, especially by the Greenland halibut fishing industry (Davis *et al.* 2013; Cosandey-Godin *et al.* 2014). Bycatch of the Greenland shark occurs by multiple methods of fishing including long-lines, trawling, and gillnets (Davis *et al.* 2013). These methods of fishing within the Arctic have become increasing popular since 2010 in order to fish for Greenland halibut, northern shrimp (*Pandalus species*), and various crab species (Davis *et al.* 2013), which means numbers of Greenland shark caught as bycatch are also increasing. According to NAFO bycatch fishery statistics, between 800 and 200 t of Greenland shark are caught as bycatch each year since 1980 (MacNeil *et al.* 2012). This statistic is troubling because a large amount of Greenland shark bycatch has been shown to be preventable. In a study by Cosandey-Godin et al., they were able to identify times and areas of higher Greenland shark bycatch risk by using Greenland halibut fishing data (Cosandey-Godin *et al.* 2013). Coastal fjord regions of western Greenland, as well as northeast Baffin Bay had 100 times higher risk of Greenland shark bycatch compared to other regions (Consandey-Godin *et al.* 2013, see fig. 6). This higher bycatch risk is most likely because these regions are thought to be pupping grounds and migration routes for the Greenland shark, as discussed earlier in the paper, so the density of Greenland sharks is high. By avoiding fishing these areas during pupping months and the migration season, a more precautionary approach can be implemented to protect Greenland shark populations.

More frequent bycatch due to increasing fishing activity in the Arctic could be detrimental to Greenland shark populations due to their life history traits. As the annual sea ice breaks up earlier each year (Stroeve *et al.* 2012), fishing industries gain more access to areas previously covered by sea ice. Access to these new fish stocks threatens Greenland shark populations as well (Davis *et al.* 2013), especially due to specific biological and physiological traits. As mentioned earlier, the Greenland shark is a K-selected species meaning growth and reproduction occur at a much slower rate than other arctic fish species (Dulvy *et al.* 2014). At less than one centimeter growth rate per year (Nielsen *et al.* 2018), the Greenland shark is at a huge risk if bycatch amounts remain constant over the next decade. Although population estimates are not available, it can be assumed that this species cannot maintain a stable population if sharks of reproductive age are continuously taken from the population. Another concerning factor regarding bycatch is that juvenile Greenland sharks are also frequently caught (MacNeil *et al.* 2012), which decreases the successful reproduction rate of the population as a whole. Increasing access to the Arctic should be met with a precautionary approach in regard to the fishing industry in order to protect Greenland shark populations and prevent a potential collapse.

Another major threat to the Greenland shark is decreasing annual sea ice extent and rising oceanic temperatures in the Arctic (Stroeve *et al.* 2012; Biastoch *et al.* 2011). Arctic spring sea ice extent is predicted to decrease somewhat dramatically over the next few decades, and this change would directly affect the amount of primary productivity in the Arctic (Stroeve *et al.* 2012; McMahon *et al.* 2006). Epontic algae and phytoplankton fuel the productivity of the benthic ecosystem in the Arctic (McMahon *et. al* 2006), so decreasing sea ice extent will in turn decrease the productivity of the benthic ecosystem. The Greenland shark spends a majority of its time in the benthic zone of the ocean while feeding (Yano *et al.* 2007), so if productivity begins to decrease, prey resources will follow. This shift from a benthic-dominated ecosystem to a pelagic-dominated ecosystem (McMahon *et al.* 2006) could potentially force the Greenland shark to spend a greater amount of time feeding at shallower depths. This species also inhabits a narrow temperature range between -1.8° C and 10° C (MacNeil *et al.* 2012) over a wide geographical area, but rising sea level temperatures could limit the area in which Greenland sharks live (Biastoch *et al.* 2011). Warmer oceanic temperatures would push the Greenland shark into more northern and/or deeper areas within the Arctic and northern-Atlantic oceans. This could not only affect population health of this species by limiting prey availability, but could also have drastic effects on the functionality of the entire Arctic marine food web.

A decreasing Greenland shark population could have major top-down effects on the Arctic marine ecosystem due to the many ecological roles this species plays. Taking into account continued harvest by Inuit communities, large numbers of bycatch by Arctic fisheries, and a biologically changing ecosystem, the Greenland shark is at major risk for population decline and potential collapse. A smaller population of the Greenland shark would have top-down effects on marine animals ranging from Arctic seal species, to Arctic cod and Greenland halibut. In order to better understand the risk of Greenland shark population decline, researchers must develop techniques to estimate region populations of this species. Without an estimate of total population, it remains unclear how aggressive bycatch protocol and restrictions should be and how protection of this species should move forward.

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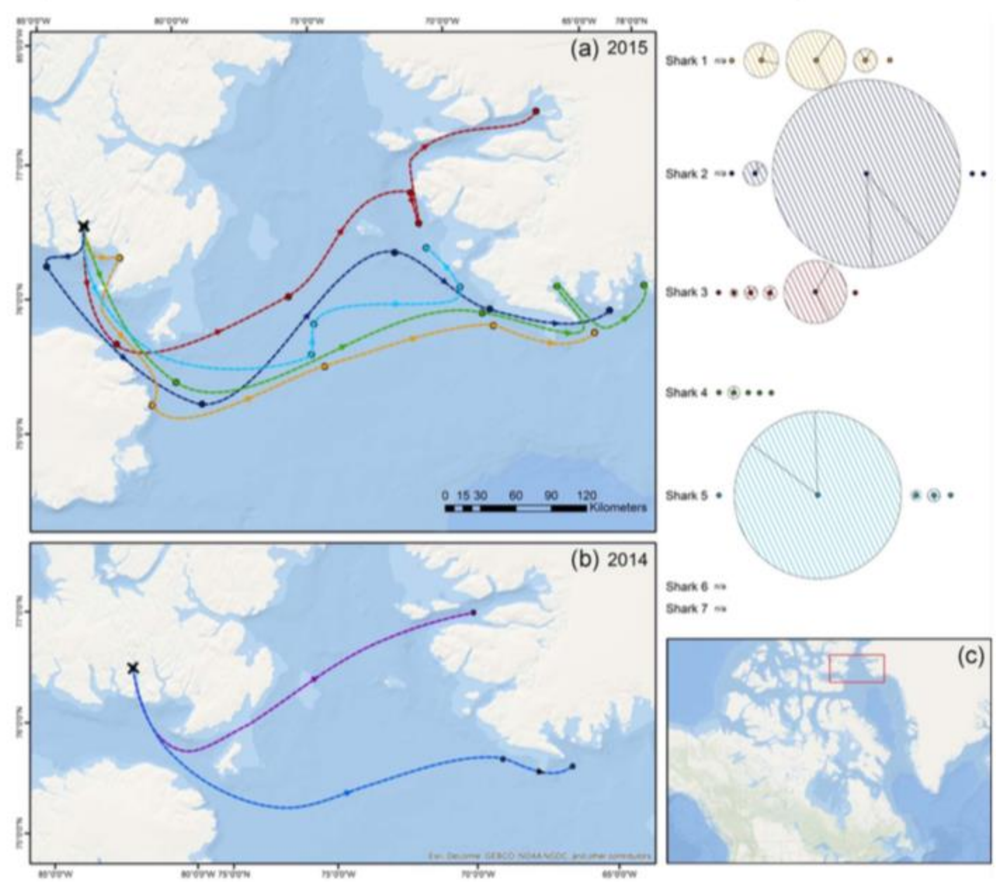

Fig. 5. Map showing directed migration of Greenland sharks from their tagging location in Steiness Fjord (marked with an 'X') to northwest Greenland. Each point indicates a pop-up location for mrPATs and miniPATs; each colour represents an individual shark and arrows indicate direction of movement. Possible location errors of the tags due to the difference in time from expected to actual report date and average drift speed are shown on the legend to the right. The triangle marked in the error circle is an indication of the likely direction from which the tag drifted and n/a values are given for tags were there was insufficient data to calculate error (too few or no locations given within a 1, 2 or 3 class). (a) Sharks tagged in 2015, (b) Sharks tagged in 2014, (c) Map of Canada and Greenland with the study location highlighted in the red box. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 1: Tracked migration patterns of the Greenland shark between north-eastern Canada and Western Greenland (Hussey *et. al* 2018).

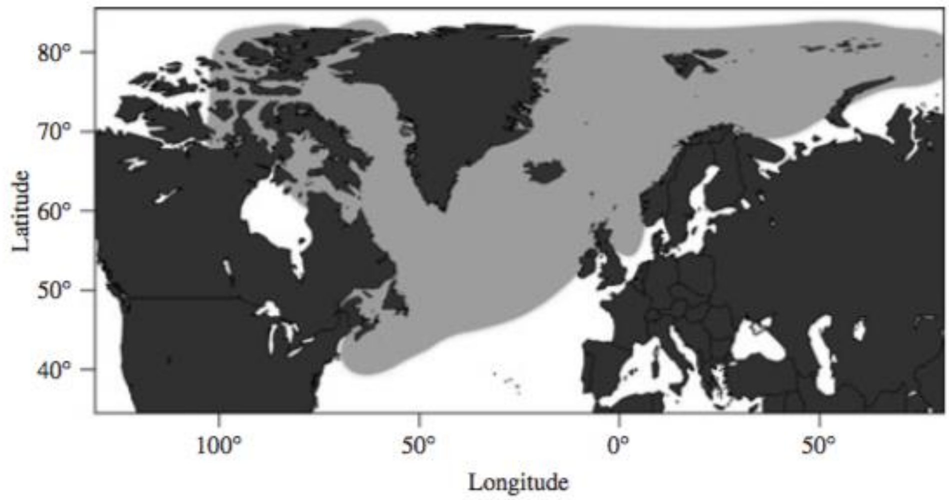

FIG. 4. Known range of Greenland shark *Somniosus microcephalus*.

Fig 2: Estimated geographic distribution of the Greenland shark (MacNeil *et. al* 2012)

TABLE II. Composition of the diet of *Somniosus (Somniosus) microcephalus* collected from West Greenland waters in terms of the index of relative importance (I_{RI}) and its components, per cent frequency occurrence (%F_O), per cent of total prey number (%N) and per cent of total contents mass (%M, g)

	Composition of the diet			
Prey	%F_O $n = 37$	%N	%M	I_{RI}
Mollusca				
Gastropoda spp	5·41	0·92	0·02	5·09
Cephalopoda				
Opisthoteuthidae spp	2·70	0·18	1·69	5·05
Octopodidae				
Bathypolypus arcticus	2·70	0·18	0·31	1·32
Unidentified squid	21·24	1·48	1·34	59·90
Unidentified cephalopod beaks	8·11	11·62	0·03	94·48
Echinodermata				
Ophiuroidea sp.	5·41	0·74	0·01	3·86
Protochordata				
Ascidiacea sp.	2·70	0·18	0·13	0·84
Coelenterata				
Scyphozoa sp.	8·11	0·55	3·16	30·09
Anthozoa sp.	5·41	2·77	0·40	17·15
Crustacea				
Decapoda				
Pandalidae				
Pandalus borealis	10·81	25·83	0·03	279·55
Oplophoridae				
Acanthephyra pelagica	2·70	0·18	0·01	0·51
Unidentified crab	2·70	0·18	0·01	0·51
Pisces				
Chondrichthyes				
Rajidae				
Raja radiata	18·92	2·03	2·43	84·38
Egg capsule	5·41	0·37	0·06	2·33
Unidentified skate	2·70	0·18	0·03	0·57
Osteichthyes				
Bathylagidae				
Bathylagus euryops	2·70	0·18	0·01	0·51
Macrouridae				
Coryphaenoides rupestris	18·92	1·85	0·38	42·19
C. guentheri	2·70	0·74	0·18	2·48
Nezumia bairdii	13·51	0·18	0·11	3·92
Gadidae				
Gadus morhua	5·41	0·37	0·41	4·22
Gaidropsarus ensis	2·70	0·18	0·11	0·78
Boreogadus saida	13·51	12·36	0·38	172·12
Scorpaenidae				
Sebastes mentella	21·62	2·40	0·64	65·72
S. marinus	10·81	1·11	1·01	22·92

Fig 3: Diet composition of the Greenland shark (Yano *et. al* 2007)

Table II. Continued

Prey	%F_O $n = 37$ (Composition of the diet)	%N	%M	I_{RI}
Cottidae				
Triglops nybelini	2·70	0·18	0·01	0·51
Artediellus atlanticus	2·70	0·55	0·02	1·54
Psychrolutidae				
Cottunculus microps	8·11	0·55	0·50	8·52
Agonidae				
Leptagonus decugonus	2·70	0·37	0·14	1·38
Cyclopteridae				
Cyclopterus lumpus	2·70	0·37	0·34	1·92
Liparidae				
Careproctus sp.	8·11	1·66	0·07	14·03
Liparis sp.	10·81	5·17	0·44	60·64
Zoarcidae				
Lycodes eudipleurostictus	5·41	0·18	0·03	1·14
Lycodonus sp.	2·70	0·18	0·03	0·57
Stichaeidae				
Leptoclinus maculatus	2·70	0·18	0·01	0·51
Anarhichadidae				
Anarhichas denticulatus	5·41	0·37	2·57	15·91
A. lupus	8·11	1·11	2·01	25·30
Pleuronectidae				
Hippoglossus hippoglossus	10·81	1·11	4·29	58·37
Hippoglossoides platessoides	2·70	0·18	0·01	0·51
Reinhardtius hippoglossoides	67·57	12·18	18·46	2070·34
Unidentified osteichthyans	27·02	6·27	2·32	232·10
Mammalia				
Pinnipedia	16·22	1·50	45·89	768·67
Phocidae				
Cystophora cristata	2·70	0·18	22·11	60·18
Phoca vitulina	8·11	0·37	18·58	153·68
Erignathus barbatus	2·70	0·18	2·26	6·59
Unidentified seals	5·41	0·37	2·94	17·91
Unidentified marine mammals	5·41	0·37	9·73	54·64
Miscellaneous				
Seaweed	2·70	0·18	0·05	0·62
Digested food or chime	8·11	0·55	0·21	6·16
Human waste				
Fishing gear and plastic bag	5·41	0·55	0·04	3·19

n, sample size.

Fig. 3 (cont.)

Fig. 2. Adult female *Ommatokoita elongata* with egg sacs attached to the cornea of a *Somniosus microcephalus*.

Fig. 4: *O. elongata* within a Greenland shark cornea (Macneil *et. al* 2012)

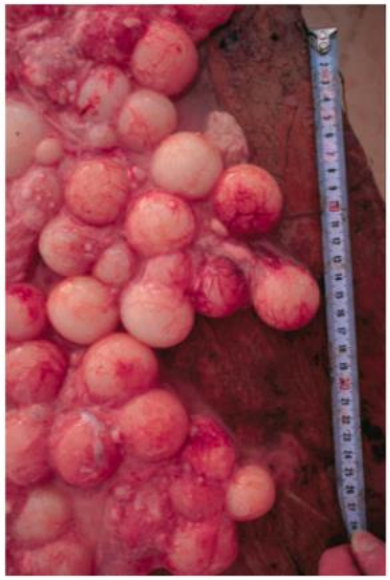

FIG. 3. Ova found in mature *Somniosus microcephalus* female in Iceland, 2003.

Fig. 5: Ova of a female Greenland shark (MacNeil *et. al* 2012)

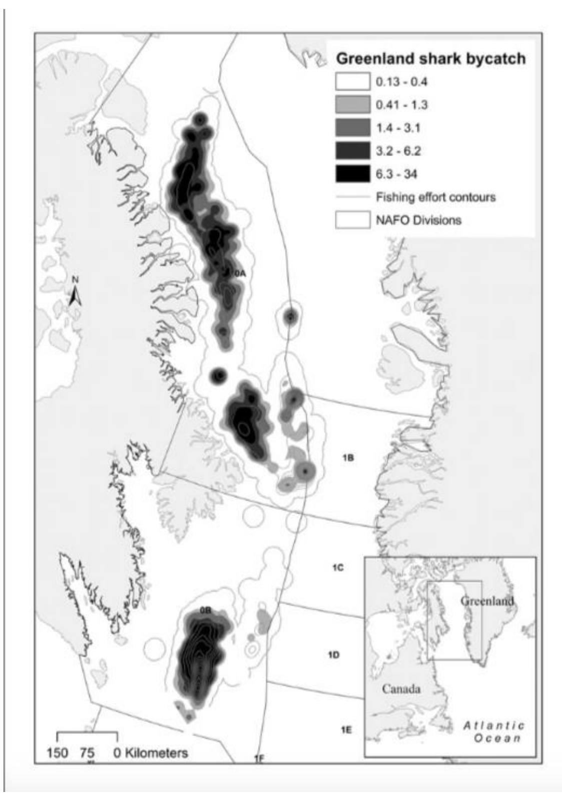

Fig. 6: Hotspots of Greenland sharks caught as bycatch by Greenland halibut fisheries (Cosandey-Godin *et. al* 2014)

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