A giant in a changing ocean: unveiling the mysteries of the Greenland shark (*Somniosus microcephalus*)

By,

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Abstract

The Arctic is a changing ecosystem that supports a wide diversity of organisms. Multi-year ice in the Arctic is declining due to warming temperatures and being replaced by thinner first year ice. This change in sea ice will have drastic effects on ice-dependent animals and sea ice algae. It is thus extremely important to get baseline data on the organisms that inhabit the Arctic waters and their food web dynamics. The Greenland shark (*Somniosus microcephalus*) is one particular inhabitant that has garnered an increasing amount of attention. This shark is the largest fish in the Arctic and it is the only shark that can withstand the cold Arctic waters year-round. It is found in deep waters down to 2,200 m throughout the Arctic Ocean and as far south as Georgia in the Atlantic. Tagging studies have revealed diel migrations under the land-fast sea ice by Greenland sharks hunting seals near their ice holes. The Greenland shark is an apex predator based on stomach content analysis preying on a number of different teleosts (Greenland halibut (*Reinhardtius hippoglossoides)* and Atlantic wolffish (*Anarhichas lupus*)), benthic invertebrates (cephalopods and crustaceans), and marine mammals (pinnepeds and cetaceans). It plays an important role in the Arctic ecosystem and could have an advantage over most Arctic predators because it is more of a generalist feeder rather than the specialist feeders like the narwhal. *S. microcephalus* could however be susceptible to bycatch if commercial fishing increases in the Arctic because of its slow growth rate and late age at maturity.

The Changing Arctic Ecosystem

The polar ice cap provides a unique habitat for organisms ranging in size from the smallest bacteria to large whales and polar bears. The ice also reflects incoming radiation from the sun back into space (Arrigo 2013). The sea ice naturally waxes and wanes throughout the year, reaching its peak extent in February at the end of winter and its minimum in September at the end of summer. Although much of the sea ice melts and declines, a large fraction has always persisted throughout the year. This ice is known as multiyear ice which is much thicker than the first year ice that reforms each winter (Arrigo 2013). In recent decades, temperature increases that have accompanied global climate change have caused most of this multi-year ice to disappear and be replaced by thinner first year ice. This first year ice has been melting earlier in the spring than usual which has allowed the ocean to absorb more solar radiation. As a result, a positive feedback system has developed (Arrigo 2013). With less sea ice to block the solar radiation, the surface temperatures have risen which melts the ice faster opening up more ocean to absorb sunlight further increasing the temperature (Perovich 2011). The volume of sea ice today in the Arctic is only 20% of what was present a few decades ago (Laxon et al. 2013). This positive feedback will continue to occur and it is no longer a question of if the Arctic Ocean will be ice free in the summer, but when (Arrigo 2013).

The loss of sea ice in the summer will affect the people of the Arctic and the organisms that live there in many different ways. Shipping companies will want to take full advantage of the Northwest Passage being completely ice free, and commercial fisheries will want to increase their efforts farther north and harvest those fish that they were unable to in the past because of the ice (Arrigo 2013). Energy companies have already begun to chomp at the bit for the opportunity to explore the shallow continental shelves for fossil fuels. With the increased activity in the Arctic, it is essential to make good management decisions in order to minimize the environmental effects these practices will have. The indigenous people of the Arctic will be impacted disastrously because they rely on the ocean for food and transportation. Access to the ice pack for hunting seals, Greenland sharks, whales and other Arctic animals is hampered as the land-fast ice (ice that is fastened to the land) diminishes and the new first year ice forms farther and farther from shore (Arrigo 2013). The Inuit rely on the ice to get to their hunting grounds and without it, their food security is in jeopardy. The northward migration of non-native species, particularly killer whales, are also taking away potential prey items from the Inuit people and the native Artic predators (Higdon et al. 2012). The loss of sea ice will have dramatic ecological effects.

Arctic species, such as pinnepeds, depend on the sea ice for food, finding mates, rearing young, and shelter (Kovacs et al. 2011). Their habitat is rapidly disappearing but it is not the only thing that will impact their survival. The base of the food web in the Arctic is made up of microscopic algae (phytoplankton and sea ice algae) that use the sunlight to produce energy (photosynthesis). The algae live in both the sea ice and the water column and provide the energy that fuels the rest of the ecosystem. Sea ice algae color the ice brown with their vast population levels and as the ice warms and melts, the algae are released into the water column where most of them sink to the bottom providing food for a rich fauna of benthic invertebrates and in turn the diving ducks, walruses and gray whales that feed on the benthos (Grebmeier et al. 2006). After the ice melts, the phytoplankton take over consuming the available nutrients in the surface ocean and growing rapidly. The phytoplankton usually far outnumber the sea ice algae, especially on the continental shelves that are very nutrient-rich (Arrigo et al. 2010). Zooplankton, such as copepods and krill, feed on the vast biomass of phytoplankton which are themselves fed upon by birds, fish, seals and whales (Loeng et al. 2005). This pattern of production and consumption is being altered by the earlier retreat and overall loss of sea ice in the Arctic. The long-term implications of this changing pattern are unclear. The loss of sea ice may increase primary production because the amount and duration of open water is increasing and the thinner first year ice lets in more sunlight for the algae to use in photosynthesis (Arrigo et al. 2008; Fortier et al. 2002; Zhang et al. 2010). The other option is lower production because the ice melt will intensify ocean stratification making it more difficult for nutrients to mix into the surface waters (Walsh et al. 2005). In the short term however, remote sensing data clearly shows primary production has dramatically increased with the loss of sea ice (Arrigo et al. 2013). Whether this production continues to increase or ends up decreasing, most of the native Arctic species are still in a dire situation with their sea ice habitat disappearing. The Arctic ecosystem is going to go through a vast remodeling as non-native species are able to migrate north through the ice free ocean and take advantage of the vast production and feed on the native species. The Arctic ecosystem is changing rapidly because of global climate change which makes it essential to learn everything we can about the interacting organisms. By establishing a baseline of studies, we can begin to predict how the food web dynamics will change and which organisms will have the upper hand.

Greenland shark

The Greenland shark (*Somniosus* microcephalus) is the only shark that lives year-round in the Arctic and is the second largest carnivorous shark in the world (behind the great white). It can reach a maximum length of about 7.3 m with female sharks growing larger than males (Yano et al. 2007). The other two members of the subgenus *Somniosus* are the Pacific sleeper shark (*Somniosus pacificus*) and the Antarctic sleeper shark (*Somniosus antarcticus*) both of which are smaller than *S. microcephalus* (Yano et al. 2007). The Greenland shark is thought to live up to 200 years making it one of the longest living vertebrates on the planet. It is very hard to age a Greenland shark because its vertebrae contain homogenous cartilage with no apparent calcification into distinct bands so conventional vertebral ageing methods are not possible (MacNeil et al. 2012). Based off a tag-recapture study, an average growth rate of 0.5 cm/year was calculated and combining that with its slow metabolic rate and an estimated 40-100 cm size at birth, a 600 cm individual may be well over 100 years old (MacNeil et al. 2012). The range of the Greenland shark extends from the temperate North Atlantic Ocean to the Arctic Ocean (Fig. 1) but this distribution has been primarily defined by observations of the species caught in cold-water commercial fisheries (MacNeil et al. 2012). Since there is no directed Greenland shark fishing in the Russian Arctic and because there are very few fisheries in the deep water south of 40^o N in the Atlantic Ocean the actual range limits of *S. microcephalus* are unknown but it is likely able to live throughout the deep sea (MacNeil et al. 2012). While exploring the shipwreck *Central America* in a submersible off the coast of Georgia (United States), a 6 m long male Greenland shark was observed and documented (Herdendorf et al. 1995). This account was the first to document the Greenland shark below 2,200 m and the Savannah, Georgia location was 440 km further south than any known records of Greenland sharks. It was also one of the deepest known photographs of a large shark. The Greenland shark is among the benthic feeding organisms in the Arctic that could be negatively affected by the loss of sea ice algae. Recent research has focused on trying to understand its place in the ecosystem and how it could be impacted in the future by the loss of sea ice.

By examining specimens, the reproductive strategies and length at maturity of Greenland sharks have gotten clearer. A total of 49 Greenland sharks were examined for size distribution, stomach content and insights into their reproduction (Yano et al. 2007). Out of the 49 bodies examined 34 were female and 15 were males. Females were larger than males with the mode for females from 400-490 cm. The reproductive strategies of the Greenland shark is largely unknown but this study provided some insight into the length at maturity for males and females. Males mature at around 300 cm and females mature at around 450 cm. The males had two equally developed testes that were ivory in color and cylindrical in shape and had a clasper that calcified when mature. The females had two equally developed ovaries with a mean of 29 pleats in the left ovary and 28.2 in the right (Yano et al. 2007). It is thought that the Greenland shark is ovoviviparous which means they give birth to live pups after the eggs have hatched inside the female. Their litters contain about 10 pups that measure around 40 cm (Strid 2010)

To date, a number of different tracking methods have been used to examine their movement patterns and residency and to formulate data on habitat, temperature preferences and hunting strategies. The tracking methods include: conventional marker tags, active or passive acoustic tracking, and pop-up satellite archival tags (Davis et al. 2013). Six Greenland sharks were tagged with a coded 32 kHz ultrasonic pressure-sensitive transmitter and their horizontal and vertical movements were tracked under the land-fast sea ice off northern Baffin Island in May (Skomal and Benz 2004). *S. microcephalus* has never been documented catching a live seal but based on previous studies of stomach contents and wounds on seals it is thought that the sharks may hunt seals near their breathing holes in land-fast sea ice. Hunting seals near their ice holes is a good opportunity because the ice-bound seals are inextricably linked to their hole with seasonally fixed dive departure and return locations that the shark could take advantage of (Skomal and Benz 2004). The pooled data for the six tagged sharks indicated nocturnal movement into shallower depths of less than 100 m between midnight and 3 am (Fig. 2) (Skomal and Benz 2004). This was followed by deeper residence during the morning hours and then a gradual shallower residence as the day went on (Fig. 2). This study was the first to use ultrasonic telemetry to track these sharks under the ice and it showed that the Greenland shark is not just a benthic predator but makes vertical migrations up to the surface below the ice which could indicate a new hunting strategy. The Greenland shark with its cryptic coloration and slow stealthy approach, likely waits under the ice near the seal's hole and strikes when they are asleep or unaware (Leclerc et al. 2012). *S. microchephalus* feeding strategy could alternate between hunting seals below the sea ice and foraging along the bottom. The seals would provide the Greenland shark with a fat-rich meal that would be sustenance for an extremely long time thus encouraging the sharks hunting behavior (Skomal and Benz 2004). Three Greenland sharks were tagged in the St. Lawrence Estuary which provided 179 days of data of the movement and habitat preferences of Greenland sharks in this estuary (Stokesbury et al. 2005). Two different electronic tagging methods were used; one shark was tagged with an acoustic telemetry tag and the other two were tagged with pop-up satellite archival tags (PSATs). The sharks exhibited a diel migration occupying mostly demersal waters during the day and then moving throughout the water column at night. The tags also indicated that Greenland sharks have a cold thermal tolerance which could allow them to forage in areas where there is no competition from other sharks. Greenland sharks come into shallow water in the summer and autumn indicating they might make seasonal migrations for feeding or reproducing (Stokesbury et al. 2005).

Feeding ecology of the Greenland shark and its role in the Arctic ecosystem

Understanding the feeding ecology of the Greenland shark is crucial for identifying the impact it could have on the Arctic food web, as well as anticipating how climate change could alter the food web properties (McMeans et al. 2013). Greenland sharks are no longer thought of as just scavengers but are able to actively stalk and kill marine mammals (Harvey-Clark et al. 2005). In terms of large predatory sharks, the Greenland shark is by far the slowest but it is capable of short bursts of speed and its cryptic coloration allows it to stalk its prey unseen (MacNeil et al. 2012). The Greenland shark is able to remove large chunks of skin and blubber from whale carcasses with its unique set of jaws. Its upper teeth are pointy but not serrated which enable the shark to pin its food into position. The bottom teeth, which are wide and curved sideways, are used to cut the food item while the shark swings its head in a circular motion. By rotating its body like an alligator, the shark cuts out a round "plug" of flesh from its prey when it is too large to swallow whole (Gallant 2013). The diet of the Greenland shark varies with its geographic location but most feed on a variety of benthic invertebrates (cephalopods and crustaceans), benthic fishes (Greenland halibut, wolffishes) and pelagic marine mammals (pinnepeds and cetaceans) (Harvey-Clark et al. 2005; Leclerc et al. 2012; Yano et al. 2007). The Greenland shark also scavenges off whale carcasses either caught in nets, like narwhals (Fig. 3) or disposed from whaling operations (Beck and Mansfield 1969). In Svalbard, Norway gastrointestinal tracts from 45 Greenland sharks were examined in order to gain insight into their impact on the local food web (Leclerc et al. 2012). Seal tissue was found in 36% of the GI tracts and whale tissue was found in 18.2%. The dominant seal prey species, based on genetic analyses, was the ringed seal (*Pusa hispida*) while the bearded seal (*Erignathus barbatus*) and the hooded seal (*Cystophora cristata*) were only found in one shark (Leclerc et al. 2012). The whale tissue was from minke whale (*Balenoptera acutorostrata*) offal, from Norweigen minke whaling operations in Svalbard that strip the blubber from the whales and throw it overboard which then float at the surface. The Greenland sharks make vertical migrations to scavenge off the minke whale offal (Leclerc et al. 2011). The dominant part of the shark's diet was fish. Atlantic cod (*Gadus morhua*), Atlantic wolfish (*Anarhichas lupus*) and haddock (*Melanogrammus aeglefinus*) being the most important fish species (Leclerc et al. 2012). The summer diet of Greenland sharks is dominated by fish in Svalbard but they are also significant active predators of seals. Their ability to feed throughout the water column on diverse types of prey makes them an important part of the Arctic food web.

One factor that could inhibit the Greenland shark's ability to feed or find its way are the parasitic copepods that attach to their corneas. The eyes of nearly all Greenland sharks are infected by the parasitic copepod *Ommatokoita elongata* (Fig. 4). The copepod attaches and feeds off the cornea of the shark which renders them nearly blind. Six Greenland shark eyes were collected in the Arctic waters of Victor Bay that were infected with the parasitic copepod *O. elongata* (Borucinska et al. 1998). Female copepods attach to the corneas of the Greenland shark via an anchoring device known as a bulla. Lesions found in the corneas of infected eyes suggest severe impairment of vision and possibly blindness. This blindness does not seem to hinder the Greenland shark's effectiveness at capturing prey as it relies more on its other senses such as olfaction, mechanoreception, and electroreception to find its prey (Skomal and Benz 2004). The Greenland shark likely evolved from deep-water squaliformes that depend more on their other senses to find prey and move around and do not have the need for an image-forming eye (Borucinska et al. 1998). Therefore, Greenland sharks impaired visually by *O. elongata* are perfectly capable of capturing prey underneath the ice in Arctic waters because, as deep-water sharks, they are adapted to both cold and low-light environments (Borucinska et al. 1998). The only population of Greenland shark that are not infected by *O. elongata* are the ones living in the St. Lawrence River. Divers observed Greenland sharks without the ocular parasites and predicted that either the parasite abundance was low in the River or the environmental conditions were not right (Harvey-Clark et al. 2005). The absence of parasites may enable the sharks in this population to have different social and investigative behaviors.

The Greenland shark's role in the Kongsfjorden (a productive fjord on the west coast of Svalbard) food web was explored to better understand its trophic interactions in a system that has been well studied in the past. Based on data using stable isotopes and fatty acids, the Greenland shark could be an important apex predator in this system by preying on a number of different seal species and fish (McMeans et al. 2013). The dominant prey species were ringed seals and Atlantic cod. The stomachs of Kongsfjorden sharks showed very little evidence of scavenging seals (few necrophageous amphipods) which lends more support to the argument that they are able to take live prey (McMeans et al. 2013). Evidence for scavenging is based off the number of necrophageous invertebrates that are found in the stomach contents of the sharks indicating predation on a dead carcass that was being eaten by other organisms. In Cumberland Sound, Canada, the Greenland halibut makes up the majority of the shark's diet which is different than the sharks in Kongsfjorden (Leclerc et al. 2012). Only using stable isotopes to look at diet analysis can be tricky and lead researchers to the wrong conclusions which is why they are paired up with another tracer: fatty acids. Combining stable isotopes and fatty acid analysis (which reflect the lipid portion of an animal's diet) provides a more complete view of the shark's diet (McMeans et al. 2013). Fatty acid analysis is used to determine the energy sources of the Greenland shark while stable isotopes were used to calculate trophic position and carbon sources for the food web (McMeans et al. 2013). Based on the results from the stable isotope and fatty acid analysis the Greenland shark is a top trophic position (4.8) consumer but its diet and potential role varies between Arctic marine ecosystems (McMeans et al. 2013). Based on the stable isotopes, 70% of their carbon was derived from phytoplankton-based food chains, which is consistent with a heavy reliance on pelagic teleosts and seals.

Another indication that the Greenland shark feeds at the top of the arctic food web is to measure their toxin levels. Dioxins (Polychlorinated dibenzo-p-dioxins and polychlorinated dibenzofurans) and PCB (polychlorinated biphenyls) concentrations were measured in 10 female Greenland sharks that were accidentally caught in trawls or entangled in long lines around Iceland (Strid et al. 2007). The Greenland shark, because of its long life span builds up high levels of toxins in its flesh. Higher dioxin levels were found in the liver (530 pg/g fat) of the 10 female Greenland sharks than in their muscle tissues (13 pg/g fat). The mean concentration of PCBs in liver (7.8 ng/g fat) in the Greenland shark specimens were similar to those reported in Polar bears that also feed at the top of the Arctic food chain (Strid et al. 2007). Greenland sharks play a unique role in Arctic marine food webs and should no longer be ignored as apex predators. Their diverse diet and large range could give them an advantage in the changing Arctic Ocean.

Potential effects of climate change on the Greenland shark

Although the Greenland shark has an advantage over most Arctic predators because it is more of a generalist feeder than a specialist like the narwhal, it could still be greatly impacted by global climate change. Climate change could impact the prey species of the Greenland shark and increase their bycatch (MacNeil et al. 2012). The benthic community that relies on the sea ice algae for their carbon source could greatly decline in the Arctic with the reduction in sea ice. Ironically, the loss of ice will most likely increase the primary productivity in Arctic surface waters which, combined with the poleward movement of warmer water species, will increase fishing effort in the Arctic Ocean (MacNeil et al. 2012). The sharks have also been hunted by the Inuit people using traditional hunting methods to provide their sled dogs and community members with meat (Davis et al. 2013). The Greenland shark is caught as by-catch in the *R. hippoglossoides* and northern shrimp *Pandalus borealis* fisheries in the north-west Atlantic Ocean. Their by-catch numbers were historically low but have tracked with the fishing effort for shrimp which has increased and decreased (MacNeil et al. 2012). With the loss of sea ice, the Arctic Ocean will be open to commercial fishing for the first time which could have profound effects on the environment and ecosystems. The Greenland shark will be at particular risk because it is slow growing, has a late age at maturity and is a member of the benthic community that will likely be fished the heaviest with trawling. The conservation of these Arctic communities should be a priority in order to preserve the unique species that inhabit the Arctic Ocean. Marine protected areas should be implemented in key arctic ecosystems to preserve the prey species that the apex predators rely on. A decline in abundance of the Greenland shark could affect the community structure of the Arctic marine ecosystems by top-down control.

Another factor that could decline the abundance of the Greenland shark is the increase of killer whales (*Orcinus orca)* in the Arctic. The vast ice cap kept the killer whales from migrating too far north but since the ice is declining, killer whales can now take advantage of prey species that are not equipped to deal with them. Killer whales prey on sleeper sharks (*Somniosus pacificus*) in the Pacific frequently, so the Greenland shark would likely be a new prey source in the Arctic along with pinnipeds (Ford et al. 2011). Indirectly the killer whales could outcompete the Greenland shark for seals which make up a large part of their diet in most populations. With killer whales potentially preying on them and outcompeting them for food and the reduction of sea ice algae, the Greenland shark could be dramatically impacted by climate change. It does however stand a chance because of its vast range and diverse diet, it will likely be able to fill niches left by other top Arctic predators (like the polar bear) or move farther south into fjords and estuaries.

Current uncertainties

There are a lot of opportunities for research on the Greenland shark to fill in the many knowledge gaps. I think we should attach National Geographic Crittercams to the backs on Greenland sharks in order to document how they are able to capture live seals. It is a mystery to me how such a large shark can sneak up and catch a seal that is a lot faster and more agile. One of the biggest challenges is to find a way to age the Greenland shark. Some scientists believe they could live over 200 years old which would make them one of the longest living vertebrates on the planet. A step toward aging them would be to do more tag-recapture studies to get a more accurate growth rate per year and see if they are continually growing throughout their lives. Very little information is known about their length at maturity, how they mate, where they go and what time of year their mating season is. If we are able to know where they mate and bear their young we can better protect them in the future. It could also give us clues as to what extent climate change will impact this unique shark species. Do they rely on the ice for mating purposes? Or do they give birth in the depths of the Arctic Ocean? I believe that when they migrate to estuaries and fjords in the summer it is mainly for mating. Using pop-up satellite tags or archival tags we can track where the sharks go at what times of year and see if they tend to travel into shallow bays during certain times of year or go to deep water to mate like great whites. More research should be done in these habitats to see if the sharks come together in large numbers to mate. The Greenland shark is a relatively unknown shark to the public but it could be one of the most important members in the Arctic food web.

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Tables/Figures

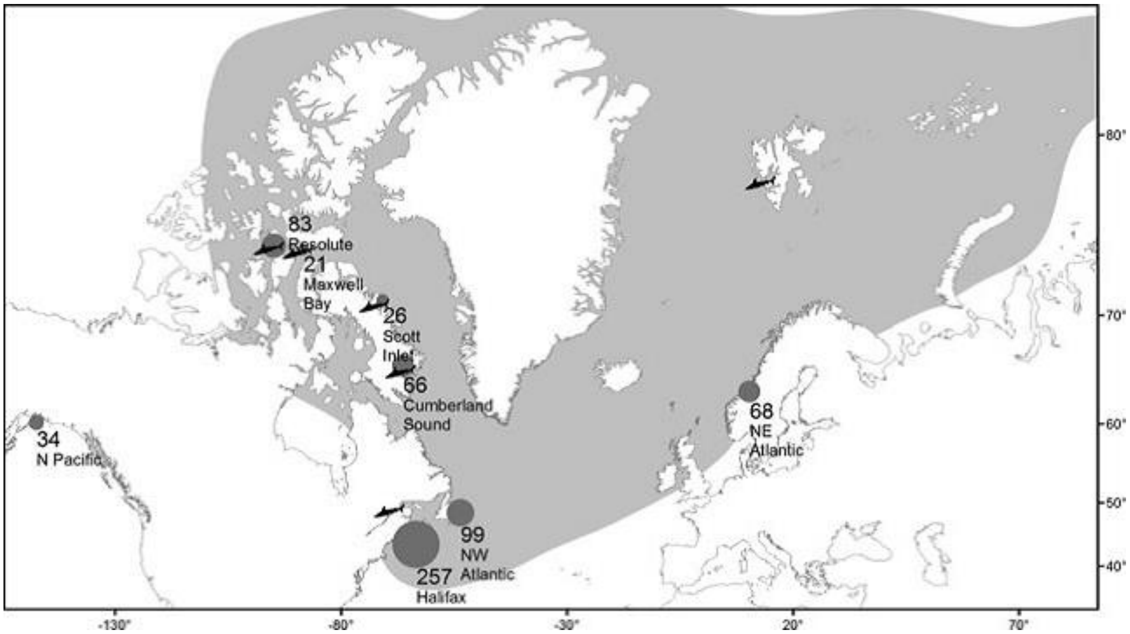

Fig 1 Greenland shark distribution and tagging efforts. Dark gray circles represent the location and numbers of Ocean Tracking Network (OTN) acoustic monitors; shark symbols represent tagging locations of Greenland sharks equipped with acoustic or satellite tags; and shaded gray area represents the known Greenland shark distribution (from Davis et al. 2013)

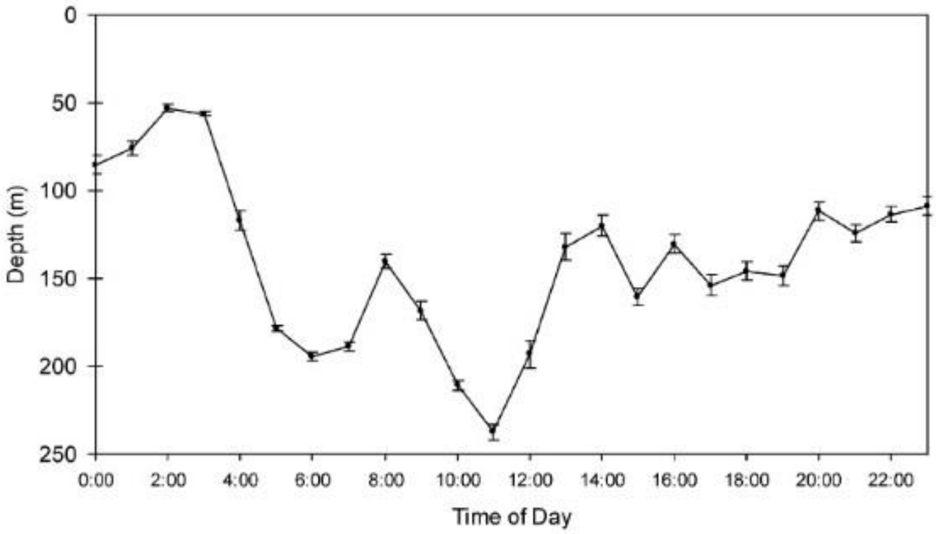

Fig 2 Diel behavior of six tracked Greenland sharks depicted by the mean (±SE) residence depth (m) (from Skomal and Benz 2004).

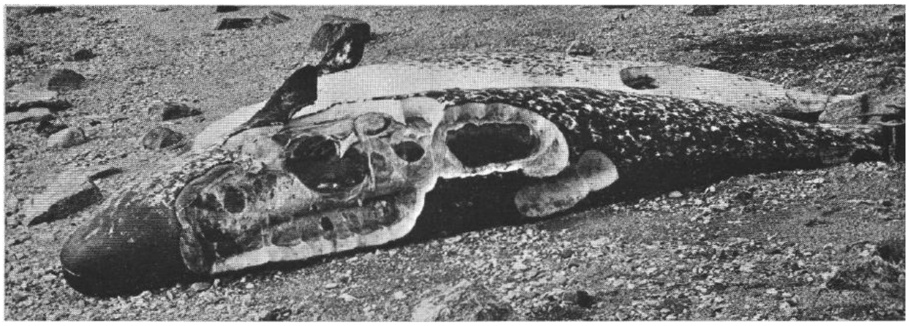

Fig 3 Narwhal attacked by a Greenland shark after being captured in nets. Note the circular bite wounds (from Beck and Mansfield 1969)

Fig 4 The eye of a Greenland shark infected with adult female Ommatokoita elongata (arrow indicates point of parasite attachment) (from Borucinska et al. 1998)