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Biology of the Greenland shark *Somniosus microcephalus*

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Greenland shark *Somniosus microcephalus* is a potentially important yet poorly studied cold-water species inhabiting the North Atlantic and Arctic Oceans. Broad-scale changes in the Arctic ecosystem as a consequence of climate change have led to increased attention on trophic dynamics and the role of potential apex predators such as *S. microcephalus* in the structure of Arctic marine food webs. Although Nordic and Inuit populations have caught *S. microcephalus* for centuries, the species is of limited commercial interest among modern industrial fisheries. Here, the limited historical information available on *S. microcephalus* occurrence and ecology is reviewed and new catch, biological and life-history information from the Arctic and North Atlantic Ocean region is provided. Given the considerable by-catch rates in high North Atlantic Ocean latitudes it is suggested that *S. microcephalus* is an abundant predator that plays an important, yet unrecognized, role in Arctic marine ecosystems. Slow growth and large pup sizes, however, may make *S. microcephalus* vulnerable to increased fishing pressure in a warming Arctic environment.

Key words: Arctic; climate change; ecology; elasmobranch; organic contaminants; parasites.

INTRODUCTION

The Arctic is experiencing climate warming more rapidly and dramatically than any other marine region (Sherman *et al*., 2009). Major primary production in Arctic waters is derived from extensive algal mats that form under seasonal sea ice each spring and are exported to the benthos during summertime ice melt (Usher *et al*., 2005). Seasonal and multi-year sea ice in the Arctic, however, has been declining steadily for many years and the area is expected to experience summer

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ice-free conditions within the next decade (Overpeck *et al*., 2005). Because of this, an important benthic food web within Arctic waters, that exists tens to hundreds of metres below the sea surface, is threatened by global warming (Carmack *et al*., 2004; Sarmiento *et al*., 2004). Paradoxically this loss of ice is expected to increase primary productivity in Arctic surface waters which, combined with a predicted poleward invasion of warmer-water species, will dramatically increase fisheries production in the Arctic Ocean (MacNeil *et al.,* 2010).

Greenland shark *Somniosus microcephalus* (Bloch & Schneider 1801) is among the benthic-feeding fishes in the Arctic that may be negatively affected by the loss of surface-exported primary production. One of only two known polar shark species, *S. microcephalus* stomach contents often contain benthic fish species, such as Greenland halibut *Reinhardtius hippoglossoides* (Walbaum 1792) (Fisk *et al*., 2002; McMeans *et al.,* 2010; LeClerc, 2011), and may be dependent on ice-related primary production. As the largest fish inhabiting Arctic waters, *S. microcephalus* may also play an important role in top-down structuring of Arctic ecosystems as marine mammals are a common diet item for the fish (Ridoux *et al*. 1998; Fisk *et al*., 2002; McMeans *et al*. 2010; LeClerc *et al*., 2011).

Historically, *S. microcephalus* has been the basis of extensive liver-oil fisheries throughout the north-east Atlantic Ocean, with sustained annual yields suggesting abundant regional populations. Yet little is known concerning their basic biology or stock status, primarily due the harshness of the Arctic environment and an absence of directed commercial fishing since the late 1960s. With the ongoing loss of multi-year sea ice leading to expanding deep-water fishing activity among native peoples, *S. microcephalus* is increasingly caught as by-catch among emerging bottom longline fisheries in the Canadian Arctic (Young, 2010). As a large, cold-bodied elasmobranch, however, it is unknown how much fishing mortality local populations can absorb.

A combination of potentially large populations, a possible role as an apex predator, and ecosystem reorganization due to climate change make it timely to explore the role of *S. microcephalus* in Arctic waters. By bringing together the current state of knowledge concerning their basic biology, this review aims to provide a foundation upon which to understand the role of *S. microcephalus* across its range and to base potential management action relevant to their conservation.

MORPHOLOGY

Many of the following observations were personal except where noted, and involved extensive use of photographs and records of all the animals collected.

DESCRIPTION

Body heavy set, cylindrical and tapering posteriorly (Fig. 1); great variability observed in overall body shape with some individuals appearing rotund while others are more elongated; large, curved, conical and posteriorly pointing dermal denticles cover entire body but not as closely spaced as in the little sleeper shark *Somniosus rostratus* (Risso 1827); snout rounded and relatively short; the upper labial furrows are not obvious except when mouth is open; predorsal length is <43% of total length, L_T (Francis *et al*., 1988); nostrils located closer to tip of snout than eye; eyes small,

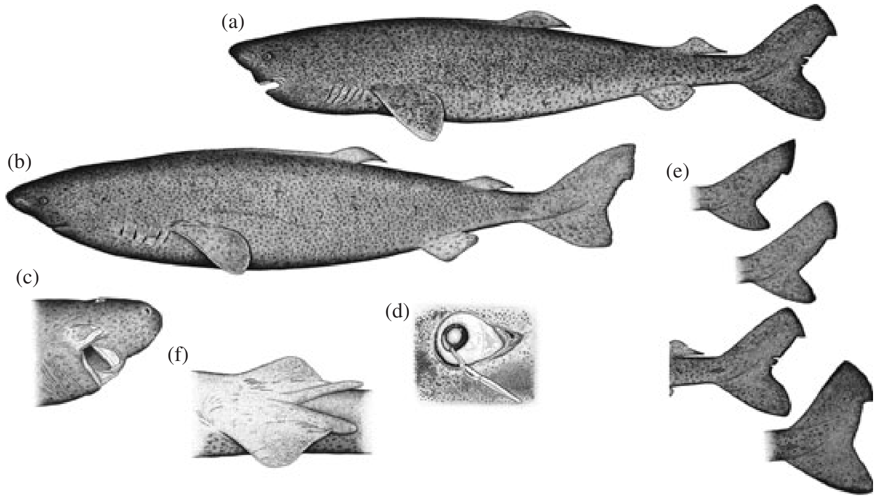

Fig. 1. (a) *Somniosus microcephalus,* (b) *Somniosus pacificus,* (c) *S. microcephalus* gape detail showing mouth protrusion, (d) *S. microcephalus* eye detail showing attached *Ommatokoita elongata* parasite, (e) range of *S. microcephalus* caudal shapes and (f) male *S. microcephalus* pelvic fin detail showing claspers.

length 5–8% of L_{T} (Yano *et al*., 2004) with a shallow notch on posterior margin; pectoral fins are small and rounded at tip and inner margin; the inner margin of pectorals is equal or longer than posterior margin; pelvic fins slightly larger in area than second dorsal fin; dorsal fins are sub-equal in size and lack spine at anterior base; the origin of first dorsal is closer to pelvic-fin base than to pectoral-fin base; the first dorsal fin is situated midway on the trunk.

A predorsal ridge extends from dorsal-fin origin anterior to origin of head; second dorsal-fin origin level with posterior part of pelvic fin, its posterior margin longer than its anterior margin; interdorsal space sub-equal to or slightly longer than prebranchial length; this contrasts with the Pacific sleeper shark *Somniosus pacificus* Bigelow & Schroeder 1944 where the interdorsal space is normally two-thirds this length; *S. microcephalus* caudal fin is epibatic (heterocercal) with the dorsal lobe being longer than the ventral lobe; a strong sub-terminal notch is present on the upper portion of the caudal fin; shape of terminal lobe is variable as is the length of the sub-terminal margin; size and shape of the caudal fin's ventral lobe is variable; ventral lobe of caudal fin is large and *c*. as wide as it is long; free rear tip of second dorsal fin not reaching caudal-fin origin; the terminal caudal lobe is sub-equal in length to the caudal fin fork width; caudal peduncle is short, rounded in cross section, with a small caudal keel slightly below the midline; precaudal pit is absent; anal fin absent.

Gill slits situated dorsolateral on head; lower teeth have clearly defined oblique cusps; lower tooth formula is (22–28)–(0–1)–(22–28); upper teeth have vertically elongated crown and roots, with crown being twice as high as the crown base width; upper tooth formula is (17–24)–(0–1)–(17–24); tooth rows 45–57 (lower) and 35–39 (upper; Yano *et al*., 2004); mouth somewhat protrusible, extending downwards beyond ventral surface of body; fork length (L_{F}) total length (L_{T}) conversion [$n = 59$; Cumberland Sound, Nunavut, Canada (65° N; 66° W)] is 1·07 ± 0·02 (mean ± s.d.; B. McMeans, unpubl. data).

COLOUR

Variable but typically light brown with dark brown mottling; specimens may be dark grey with darker, near-black mottling; dark to black colouration is sometimes visible along the anterior margin of the pectoral and caudal fins; intensity and pattern of mottling covering entire body is variable; the ventrum is usually as dark as the dorsum; mucous layer may give specimen a violet tinge when not in water; many specimens take on a dark-blue appearance out of water; white spots have been reported on some specimens (Castro, 1983); although similar in overall colouration, mottling on *S. pacificus* is usually less distinctive; some specimens have small spotting over entire body and fins; Drainville (1960) reported *S. pacificus* colouration to be bluish-grey once the mucous layering (epidermis) has been rubbed off, also noting numerous, but subtle black transversal bands; colour is variable and affected by whether specimen is viewed underwater or out of water.

SIMILAR SPECIES

Somniosus pacificus most closely resembles *S. microcephalus* and distinguishing the two species based on external morphology is difficult. The former is brownish in overall appearance. Francis *et al*. (1988) reported that once the external mucous covering is rubbed off, *S. pacificus* takes on a pink-grey colouration with blue-black edges on all fins. The caudal keel is not a useful diagnostic character since it is present in some but not all specimens of *S. pacificus* (Francis *et al*., 1988). Predorsal length is more than 43% of L_T. Tooth:row formula (upper:lower) for *S. pacificus* is usually 30–48:46–63 while *S. microcephalus* is 35–39:45–57. *Somniosus microcephalus* can be distinguished from small Portuguese shark *Centroscymnus coelolepis* Barbosa du Bocage & de Brito Capello 1864 specimens by a lack of spines in its dorsal fins and more lunate caudal fin. *Centroscymnus coelolepis* rarely exceeds 100 cm L_T. The bramble shark *Echinorhinus brucus* (Bonnaterre 1788) can reach sizes more comparable with *S. microcephalus,* but has its first dorsal fin originating more posteriorly, in line with the midpelvic base and is covered by dermal platelets, each with a sharp, anterior pointing hook. Recent analysis of phylogentic relationships between *S. microcephalus, S. pacificus*, as well as *S. antarcticus* using mitochondrial *cytochrome b* variation suggested that *S. microcephalus* is a distinct species from *S. pacificus* and *S. antarcticus,* with the last two species highly similar (Murray *et al.,* 2008).

PHYSIOLOGY

Somniosus microcephalus physiology is not generally well studied. Some insights on chemical physiology have been generated due to perceived toxicity originating in reports from the mid 20th Century (see below; McAllister, 1968; Coad, 1995).

Somniosus microcephalus, and the related spiny dogfish *Squalus acanthias* L. 1758, have among the highest levels of trimethylamine *N*-oxide (TMAO) on record (Seibel & Walsh, 2002). Anthoni *et al*. (1991) found that *S. microcephalus* flesh had TMAO concentrations between 1·05 and 1·30 g 100 g^{-1}, well within the reported 0·864–1·69 g 100 g^{-1} range observed for *S. acanthias* (Goldstein *et al*., 1967; Bedford *et al*., 1998). While the role of TMAO is not fully understood (Seibel & Walsh, 2002), the high levels found in polar fishes indicate that this osmolyte may increase osmotic concentrations to depress the freezing point of body fluids. In addition, TMAO and its reduced form trimethylamine (TMA) are large, positive, low-density molecules that may improve buoyancy. Moreover, TMAO acts as a counteracting solute that protects proteins against destabilizing forces such as the high urea concentrations present in elasmobranchs and the high hydrostatic pressures generally experienced by deep-sea animals (Seibel & Walsh, 2002). Although the exact role of TMAO in *S. microcephalus* is unknown, the fish's distribution and life history suggest many of the potential functions above may apply.

The lipid content of *S. microcephalus* livers from Cumberland Sound (collected in 1998, 1999, 2007–2009, $n = 66$, mean ± S.D. $L_T = 291 \pm 34$) and Davis Strait (collected in 1997, $n = 2$, L_T both 135 cm) have been documented previously (Fisk *et al*., 2002). Neutral lipids of the livers by mass in the larger Cumberland Sound fish were 67·7 ± 16·7% (mean ± S.D.), while two smaller Davis Strait specimens had lipid content of 36 and 43%, respectively. Studies on *S. pacificus* livers have shown that diacylglyceryl ethers and triacylglycerols, respectively, represent 50 and 49% of the lipid composition of the liver (Bakes & Nichols, 1995). Contrary to other shark species, both *S. acanthias* and *S. pacificus* show no evidence of squalene in their liver (Malins & Barone, 1970; Bakes & Nichols, 1995). Diacylglyceryl ethers and triacylglycerols are thought to act in concert, or together with other lipids, as buoyancy regulating molecules in shark livers (Malins & Barone, 1970). Presumably, similar analysis of *S. microcephalus* liver would reveal a composition close to that of *S. acanthias* and *S. pacificus.*

Although elasmobranch immune systems have been relatively well-studied in general (Flajnik & Rumfelt, 2000), there is comparatively little known of the immune system of *S. microcephalus* or any other polar shark. High lysozyme activity levels found in the Leydig organ, spleen and pancreas of *S. microcephalus* suggest a well-developed immune response in this species (Fange *et al*., 1980). A unique lysozyme, β-N-acetylglucosaminidase, was found in the Leydig organ and ovaries of *S. microcephalus* that might provide immune function against bacteria and parasites (Fange *et al*., 1980). Beyond this, however, very little is known.

Element data collected from *S. microcephalus* livers in Cumberland Sound ($n =$ 24) have shown that arsenic, cadmium, selenium and mercury concentrations appear to vary little between sexes and are not related to L_T (McMeans *et al*., 2007). Arsenic and cadmium were found at the highest concentrations (9·8 ± 0·7 and 3·9 ± 0·4 $\mu g\ g^{-1}$, mean ± S.E.,) followed by selenium (0·52 ± 0·03 $\mu g\ g^{-1}$), mercury (0·49 ± 0·06 $\mu g\ g^{-1}$) and lead (below detection limits of 0·002 $\mu g\ g^{-1}$). Concentrations of total mercury in *S. microcephalus* liver (0·49 ± 0·06 $\mu g\ g^{-1}$) were more than an order of magnitude greater than sea-run Arctic charr *Salvelinus alpinus* (L. 1758) muscle collected in Cumberland Sound, but several orders of magnitude less than levels observed in marine mammal livers (Fisk *et al*. 2003).

ORGANIC CONTAMINANTS IN *S. MICROCEPHALUS*

Recently, there have been a number of studies that have reported concentrations of organic contaminants, such as polychlorinated biphenyls (PCB), dichlorodiphenyltrichloroethanes (DDT) and polybrominated diphenyl ethers (PBDE) in *S. microcephalus* from North Atlantic waters (Fisk *et al*., 2002; Strid *et al*., 2007, 2010).

In general, contaminant concentrations were high in *S. microcephalus*, which is not surprising given its high trophic position, large size and residence in colder waters. Contaminants are found in the Arctic at significant levels due mainly to the long-range transport of these chemicals from temperate regions (Fisk *et al.*, 2003; de Wit *et al.*, 2004). Many contaminants (*e.g.* PCBs and mercury) biomagnify up marine food webs, achieving their greatest concentration among top predators (Muir *et al.*, 1988; Fisk *et al.*, 2001). Contaminants such as PCBs also tend to increase with fish size (Johnston *et al.*, 2002). Concentrations of organochlorine contaminants (OC), however, have not been significantly related to size of *S. microcephalus* sampled from Cumberland Sound (Fisk *et al.*, 2002).

Concentrations of PCBs (reported as ΣPCB, the sum of individual PCB congeners) in *S. microcephalus* livers were slightly higher in fish collected from Iceland (ΣPCB = 4400 (range 990–10 000) ng g^{-1} lipid; lipid % = 55 (35–72); Strid *et al.*, 2007) than from Cumberland Sound (ΣPCB = 3442 ± 650 ng g^{-1} lipid; lipid % = 56 ± 2·1; mean ± S.E.). The difference may be even greater than this as Fisk *et al.* (2002) measured a much larger number of PCB congeners; however, differences between locations probably reflect a combination of higher contaminant levels in the waters to the east of Greenland (de Wit *et al.*, 2004) and larger size of Icelandic *S. microcephalus*.

Strid *et al.* (2007) reported that PCB concentrations, on a lipid basis, were similar between muscle and liver in *S. microcephalus*, a common observation in fishes (Janz *et al.*, 1992) but not always in sharks (Gelsleichter *et al.,* 2005). Concentrations of ΣDDT and Σ chlordane pesticides in Cumberland Sound *S. microcephalus* livers were 7159 ± 1271 and 1815 ± 273 ng g^{-1} lipid mean ± S.D. (Fisk *et al.*, 2002); polychlorinated dibenzo-p-dioxins and furans (PCDD; PCDF) in Iceland *S. microcephalus* livers were 0·071 and 0·460 ng g^{-1} lipid. These concentrations are the highest reported for an Arctic fish and are in the range of top Arctic marine predators such as polar bear *Ursus maritimus* (Norstrom *et al.*, 1998) and glaucous gull *Larus hyperboreus* (Buckman *et al.,* 2004).

Recently, Strid *et al.* (2010) reported on concentrations of natural and anthropogenically-derived brominated compounds in livers of 10 *S. microcephalus* collected around the waters of Iceland. Levels of PBDEs, anthropogenic-origin, and natural brominated compounds (2,4,6-tribromophenol) were higher in *S. microcephalus* than in other fish species collected around Iceland; this was attributed to their higher trophic position, large size and possibly also high longevity. None of these compounds were correlated to L_T, similar to other contaminants.

Somniosus microcephalus have a unique profile of contaminants that reflect omnivorous feeding, a potentially limited ability to biotransform chemicals, and a potentially long life. Many low chlorinated PCB, and PCDD and PCDF congeners, those with two or three chlorines, have been found in *S. microcephalus* tissue (Fisk *et al.*, 2002; Strid *et al.*, 2007). These contaminants are generally biotransformed and eliminated in higher trophic level organisms, particularly birds and mammals (Muir *et al.*, 1992). Examination of PBDE congeners also suggested limited biotransformation capacity in *S. microcephalus* (Strid *et al.,* 2010). It has been suggested that sharks have limited capacity to biotransform contaminants in general (Johnson-Restrepo *et al.,* 2005), and *S. microcephalus* may have an exceptionally low capacity given its preference for cold waters.

Curiously, *S. microcephalus* have higher levels of DDT than its metabolized form dichlorodiphenyldichloroethylene (DDE) (Fisk *et al.*, 2002). Because DDT is converted to DDE in the environment, DDE is usually much higher than DDT in Arctic organisms (de Wit *et al.*, 2004). High DDT levels in *S. microcephalus* seem to still occur despite the fact that DDT use has been severely reduced since the 1970s and the Arctic is removed from major DDT sources. Therefore the high DDT levels observed suggests limited biotransformation capacity in *S. microcephalus* and exposure to DDT prior to the 1970s. Finally, oxychlordane, a metabolite of chlordane normally found only in birds and mammals, is also prevalent in *S. microcephalus* and probably reflects their habit of feeding on marine mammals (Fisk *et al.*, 2002), as well as their limited biotransformation capacity.

TOXICITY OF *S. MICROCEPHALUS* FLESH

A number of publications have referred to the toxicity of *S. microcephalus* (Bøje, 1939; McAllister, 1968; Coad, 1995); its muscle tissue is considered inedible by Inuit in the Canadian Arctic (A.T. Fisk, pers. obs.). Sled dogs in Greenland that had been fed raw *S. microcephalus* tissue were reported to walk with slow stiff steps, hypersalivate, vomit, have muscular convulsions, respiratory distress, explosive diarrhoea and, in some cases, die (McAllister, 1968). It has also been reported that ravens *Corvus corax* and northern fulmars *Fulmarus glacialis* seen scavenging on *S. microcephalus* could not subsequently fly and often stumbled around as though intoxicated (Coad, 1995).

In 1996, 15 hungry sled dogs were fed on *c*. 68 kg of *S. microcephalus* flesh (muscle and skin) that had soaked in $-1{\cdot}7^{\circ}$ C water for 9 days (possibly eliminating any toxicity). All animals ate to satiation, consuming all but 13–23 kg of meat. The dogs were watched through the day following feeding with no noticeable aberrant behaviour. Inuit guides in Arctic Bay, Nunavut, reported that, although not used as food, *S. microcephalus* is not toxic; team members consumed small amounts (*c*. 5 g) of flesh with no ill effects. Johansen (2002) notes that quantity is the key aspect for toxicity and an adult would have to consume in the order of 20 kg of *S. microcephalus* meat in one sitting before experiencing the symptoms described above.

The single effort to assess whether *S. microcephalus* flesh actually contained a toxin suggested trimethylamine-oxide (TAMO) as a probable source (Anthoni *et al.*, 1991). They hypothesized that the toxicity of TMAO was due to acute trimethylamine (TMA) poisoning when TMAO is reduced to TMA in the gut of a consumer. Mice and rats injected with TMA showed symptoms similar to those observed in dogs that had been attributed to *S. microcephalus* intoxication. TMAO has a low toxicity, however (LD50 >2850 mg kg^{-1} in mammals), and a massive ingestion of tissue would be required to elicit symptoms. Anthoni *et al.* (1991) noted that these symptoms could arise if infrequently fed sled dogs were allowed to gorge themselves on fresh *S. microcephalus* meat. It may well be that the consumption of large amounts of any marine elasmobranch would elicit toxic effects, as TMAO is a common chemical in shark meat.

A second possible source of flesh toxicity that has been suggested for these fish is their consumption of small shell-less molluscs (pteropods) by (McAllister, 1968). This theory has arisen because *R. hippoglossoides* and shorthorn sculpin

Myoxocephalus scorpius (L. 1758) sometimes elicit symptoms similar to shark intoxication when those species have heavily ingested pteropods. This hypothesis has not been tested to date, however, and any potentially toxic species of pteropod have not yet been identified.

A final possible explanation for toxicity in *S. microcephalus* flesh could be high contaminant concentrations. Although many contaminants can illicit toxic effects, it is usually at high concentrations (Fisk *et al*., 2002). But consuming even a large amount of *S. microcephalus* tissue, as was the case for the sled dogs, would not be sufficient to elicit the toxic responses associated with consumption of contaminants and would require long-term consistent consumption of the tissue to achieve levels that would be toxic. As a comparison, *U. maritimus* consume seals that have similar contaminant levels to *S. microcephalus*. Although some toxic effects related to contaminants have been reported in *U. maritimus* (Letcher *et al.,* 2010), behaviour similar to 'shark drunk' has not been reported.

PARASITES

Among the most obvious and distinctive characteristics of *S. microcephalus* is the frequent presence of the ectoparasitic copepod *Ommatokoita elongata* that attaches to and freely dangles from the shark's cornea (Grant, 1827). The parasite is intriguing not only because of its large size (adult females with egg sacs commonly reach 4–6 cm; Fig. 2; Kabata, 1979) and site of attachment, but also because of its high frequency of occurrence. Berland (1961) reported that the eyes of 98·9% ($n = 1505$) of *S. microcephalus* caught from East Greenland carried *O. elongata*, and 100% ($n = 6$) from northern Baffin Island were infected (Skomal & Benz, 2004). *Somniosus microcephalus* from Cumberland Sound and Svalbard, Norway, had 73% ($n = 15$) and 100% ($n = 46$) infection by *O. elongata,* respectively, on one or both eyes. In contrast, the four *S. microcephalus* observed by Harvey-Clark *et al*. (2010) from the St Lawrence River, Canada, were uninfected, and these authors suggest that St Lawrence fish are less frequently infected than their Arctic conspecifics. It seems more common than not, however, that *S. microcephalus* have *O. elongata* attached to their corneas, which raises obvious questions about how the parasite physically affects the fish, and how the fish survives with potentially impaired vision. To date, several studies have investigated how *O. elongata* affects *Somniosus* spp. corneas, and subsequently, how the fish's vision could be affected (Borucinska *et al*., 1998; Benz *et al*., 2002).

Ommatokoita elongata is confirmed to infect only *S. microcephalus* and *S. pacificus* (Benz *et al*., 1998). One *O. elongata* adult female typically infects each eye, and attaches by inserting an anchoring device, the bulla, into the fish's cornea (Borucinska *et al*., 1998). The copepod swings freely about this anchor point and, using its maxillipeds to grasp the surface of its host, can feed on cornea or conjunctiva within the radius of its mouth tube (determined by the length of its second maxillae; Borucinska *et al*., 1998; Benz *et al*., 2002). The avascularity of the cornea, and therefore lowered immune response, probably allows adult female *O. elongata* to remain affixed to a host's eye for a substantial period of time (Benz *et al*., 2002). In addition to an adult female, *S. microcephalus* corneas may also host one to several *O. elongata* larvae (Borucinska *et al*., 1998) that attach using a frontal filament anchored by a distal plug (Benz *et al*., 2002).

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

The area surrounding *O. elongata's* attachment site is visibly opaque (Borucinska *et al*., 1998; Benz *et al*., 2002). Histologically, insertion of the bulla by adult females results in severe alterations to the cornea, including ulceration of corneal epithelium and thinning and mineralization of corneal stroma (Borucinska *et al*., 1998). Opaque bands are also apparent on the periphery of infected corneas and are thought to occur from feeding and abrasion by the copepod's body (Borucinska *et al*., 1998). Damage observed surrounding distal plugs and frontal filaments of *O. elongata* larvae infecting *S. pacificus* eyes included disorganization of corneal epithelium, and oedema and inflammation of stroma (Benz *et al*., 2002). In addition to active infection sites, multiple scars or opacities may also be present on the cornea. Bullae were not found within these opacities in the six *S. microcephalus* investigated by Borucinska *et al.* (1998), but Benz *et al.* (2002) reported that one to several opaque sites on nine *S. pacificus* eyes (out of 20) contained a bulla, confirming that these lesions can result from previous *O. elongata* infections.

The damage to *S. microcephalus* cornea and loss of transparency that results from active and previous *O. elongata* infections and from feeding and abrasion, suggest that *O. elongata* severely inhibits the vision of, or even blinds, its host (Borucinska *et al*., 1998; Benz *et al*., 2002). Specifically, the eyes of infected *S. microcephalus* are considered capable of only light reception and rough image formation (Borucinska *et al*., 1998). Such poor vision might be expected to decrease the foraging success of *S. microcephalus*, however, Borucinska *et al.* (1998) suggested that *S. microcephalus* may not rely heavily on vision for survival. Other senses, like olfaction, which is highly developed in this species may compensate for diminished vision, especially in low light environments like deep water (Borucinska *et al*., 1998) or ice-covered seas.

As discussed later, *S. microcephalus* are numerous in Arctic seas and are clearly capable of capturing live prey. Thus, infection by *O. elongata* is a characteristic feature, though not ubiquitous or overly detrimental, of *S. microcephalus* biology (Harvey-Clark *et al.,* 2010).

LIFE HISTORY

Records of *S. microcephalus* reproduction are limited and infrequent. In a review of their reproduction, Bjerkan (1957) discussed the idea that *S. microcephalus* was oviparous, with females containing high numbers of large soft eggs and no embryos having been found. Koefoed (1957), however, reported finding two embryos in utero. The first, a 98 cm specimen whose mother was caught in a Norwegian fjord, was discarded before examination. The second, examined by Koefoed (1957) was from a 500 cm female caught near the Shetland Islands, U.K. Koefoed (1957) noted that the 37 cm L_T embryo showed no evidence of a yolk sac and had no connection with the uterine mucosa, meaning that the pup was close to term. On the basis of this specimen and the apparent absence of a shell gland, it has been thought that *S. microcephalus* is viviparous (Koefoed, 1957). Numerous *S. microcephalus* with fertilized eggs in utero, including a female from Cumberland Sound that contained *c.* 1800 fertilized eggs have been observed (unpubl. obs.). Yano *et al.* (2007) also noted that three female *S. microcephalus*, all >400 cm L_T, had 2689, 2922 and 2931 ova. *Somniosus microcephalus* is therefore capable of producing yolk-dependent offspring (Carrier *et al.,* 2004).

The size at birth and gestation period of *S. microcephalus* remains unknown. Based on two embryos (37 and 98 cm L_T) from different locations, Bjerkan (1957) concluded that size at birth varies greatly. In support of this conclusion they cited the observations of Collett (1905), who reported that the smallest free-swimming *S. microcephalus* that had been observed were 60–100 cm L_T; Bigelow & Schroeder (1948) reported a free-swimming specimen of only 45 cm. More recently, Kondyurin & Myagkov (1983) described two 100 cm *S. microcephalus* captured in a midwater (250–300 m deep) trawl near Jan Mayen Island, Norway. On the basis of the remnants of an external yolk sac and the presence of yolk residues in the digestive organs, they concluded that the fish were 10–15 days old and that parturition occurred in the Norwegian Sea during July and August. This record contradicts Koefoed's (1957) suggestion that the yolk sac is completely absorbed in utero. In 2002, Kukuev & Trunuv (2002) captured the two smallest known free-swimming *S. microcephalus* near Iceland; one of these measured 42 cm and was captured near the Reykjanes Ridge (62° N; 26° W), while the other 47 cm specimen was taken in late June from the Irminger Current above the western slope of the Reykjanes Ridge. Kukuev & Trunuv (2002) assumed, based on their size, that both animals were neonates, but did not examine the fish internally. Based on previous reports and a single 41·8 cm L_T *S. pacificus* captured from Japan, Yano *et al.* (2007) conclude all three *Somniosus* spp. have a 40 cm L_T size at birth. Assuming the aforementioned fishes were properly identified, size at birth for *S. microcephalus* probably lies between 40 and 100 cm.

With few published records it is difficult to determine the size at maturity of this species. Bigelow & Schroeder (1948) noted that males at 183 cm were immature. Dunbar & Hildebrand (1952) reported the clasper characteristics of two males with conflicting results; a 290 cm long male had well-developed claspers while a larger 371 cm male possessed only small rudimentary nodules. These results are similar to observations of males from Victor Bay, Canada (73° 06′ N; 85° 15′ W) and Cumberland Sound where fish, between *c*. 260 and 320 cm L_T, have either possessed well developed, calcified claspers indicative of reproductive maturity, or claspers that were poorly developed and, upon internal examination, found to be immature (pers. obs.). Further confounding this issue, Beck & Mansfield (1969) examined nine males ranging from 237 to 311 cm caught off northern Baffin Island and concluded that all were immature based on a histological examination of testis tissue. Yano *et al.* (2007) examined 13 male *S. microcephalus* and suggested males approach maturity *c*. 300 cm based on a rapid increase in clasper size at this length. They also noted that a 311 cm male had calcified claspers. Therefore, the onset of sexual maturity in male *S. microcephalus* probably occurs at *c*. 260 cm, but this appears to be highly variable.

While numerous authors have described the presence of large eggs (Bjerkan, 1957), information on size at maturity for female *S. microcephalus* is lacking. Beck & Mansfield (1969) examined eight females ranging from 217 to 295 cm and concluded that all were immature as no eggs were visible in the ovaries. A female that contained a single embryo examined by Koefoed (1957) was 500 cm L_T. Mature females from Iceland have been between 355 and 480 cm L_T (unpubl. data). The ova within these animals were large (6 cm; Fig. 3) and numbered into the hundreds per individual. Yano *et al.* (2007) has suggested that female *S. microcephalus* approach the onset of maturity at >400 cm based on a change in ovary mass.

DISTRIBUTION AND HABITAT

The known range for *S. microcephalus* extends from the temperate North Atlantic Ocean to the Arctic Ocean (Fig. 4), a distribution that has been defined primarily by observations of the species caught in cold-water commercial fisheries (unpubl. data). Because there has been no directed fishing for *S. microcephalus* in the Russian Arctic and because few fisheries exist in deep water south of 40° N in the Atlantic Ocean, few conclusions can be drawn about the actual range limits of *S. microcephalus*. Given their tolerance for extreme cold water and their ability to inhabit abyssal depths, the range for *S. microcephalus* is potentially unlimited throughout the deep sea.

Somniosus microcephalus has most frequently been caught in deep water surrounding Greenland as part of directed fisheries for shark liver oil during the first half of the 20th Century (Jensen, 1948; Templeman, 1963). Exploratory bottom-longline sets in the Canadian Arctic Archipelago, west Baffin Island and in Hudson Strait failed to capture either this fish or its potentially important *R. hippoglossoides* prey (D. Evic, pers. comm.). These exploratory sets have, however, been limited in duration and have used gear more suited to catching flatfishes. There is, therefore, only weak evidence of substantial range limitation through the Canadian Archipelago. The northern range limit of *S. microcephalus* is not known as it extends into areas of the Arctic Ocean that have historically been covered by multi-year sea ice. The eastern range limit is also unknown although the fish is sometimes caught in deep-water fisheries in the Barents Sea. Reports of *S. microcephalus* outside the north-west Atlantic Ocean

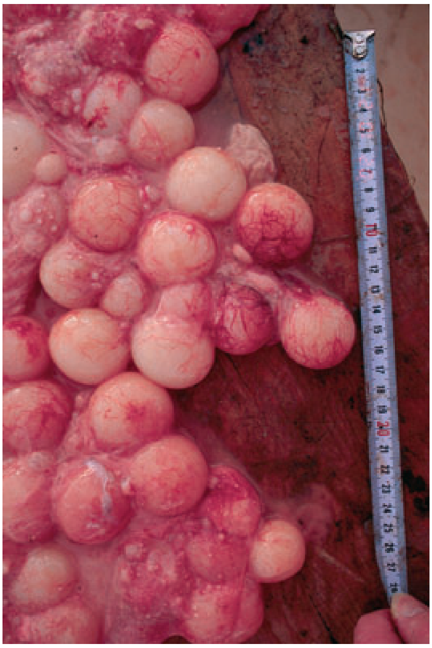

FIG. 3. Ova found in mature *Somniosus microcephalus* female in Iceland, 2003.

should be considered cautiously due to the difficulties in distinguishing it from *S. pacificus* (Benz *et al*., 2007).

Specific observations of *S. microcephalus* have occurred in waters off Norway (Bjerkan, 1957; Pawson & Vince, 1999), Iceland (Magnússon & Magnússon, 1995; Ridoux *et al*., 1998; Pawson & Vince, 1999), west Greenland (Jensen, 1948; Berland, 1961), Baffin Island (Fisk *et al*., 2002; Skomal & Benz, 2004), eastern Quebec (Dunbar & Hildebrand, 1952; Drainville, 1960; Stokesbury *et al*., 2005), Newfoundland

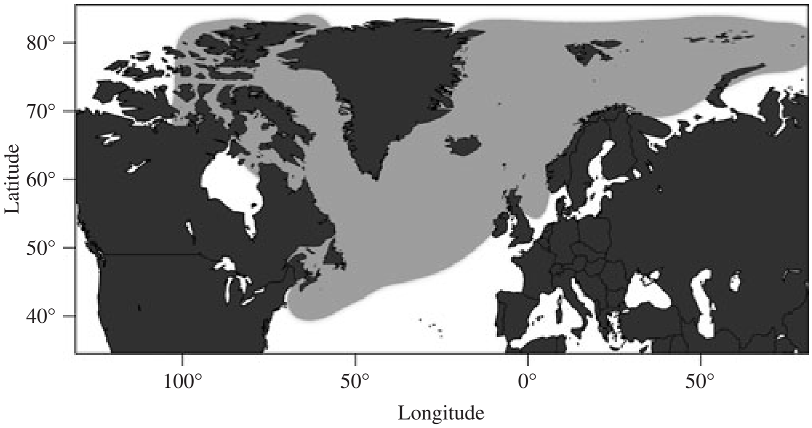

FIG. 4. Known range of Greenland shark *Somniosus microcephalus*.

(Templeman, 1963) and Nova Scotia (Templeman, 1963; Joyce, 1999). Infrequent observations have occurred off France (Quero *et al.*, 1984) and in the Gulf of Maine (Bigelow & Schroeder, 1948).

Observations of *S. microcephalus* south of 42° N in the Atlantic Ocean are rare and have not been well substantiated due to difficulties in *Somniosus* spp. identification (Benz *et al.*, 2007). A 440 cm *Somniosus* sp. was captured in a 1967 trawl at 667 m off South Africa (32° 50′ S) that was reported to be *S. microcephalus* (Bass *et al.*, 1976); the reported 48:53 tooth formula make it difficult to discern whether the specimen was indeed *S. microcephalus* or *S. pacificus*. In 1990, a 600 cm L_T male *Somniosus* sp. captured on still camera 370 km east of Savannah, Georgia, at 2200 m depth in 2° C water was reported to be *S. microcephalus* (Herdendorf & Berra 1995). In 2001, a 240 cm *Somniosus* sp. individual was observed by remote operated vehicle (ROV) at 2647 m in the Gulf of Mexico (Benz *et al.*, 2007). Finally, a 420 cm L_T male *S. microcephalus* from 800 m depth off the continental shelf of Argentina has been reported, but identification was confounded by the frozen specimen having badly damaged upper teeth and a lower tooth pattern closer to *S. pacificus* (Francis *et al.*, 1988). Therefore there have been no validated reports of *S. microcephalus* from the southern hemisphere.

Somniosus microcephalus shows a marked preference for cold water; all recorded catch and observation temperatures have been from $-1{\cdot}8$ to $10{\cdot}0°$ C (Bigelow & Schroeder, 1948; Stokesbury *et al.*, 2005; pers. obs.), with most records having been from water $<5°$ C. Aside from their consistent affinity with cold temperatures, little is known about the habitat preferences of *S. microcephalus* as the majority of observations have been from by-catch in demersal longline fisheries. Observations have occurred both inshore, in water <1 m in depth, and offshore, at abyssal depths >1200 m (Yano *et al.*, 2007).

One of the few repeated habitat associations for *S. microcephalus* has been their presence in fjords, including those in Norway (Bjerkan, 1957; Koefoed, 1957; Coad, 1995), Greenland (Jensen, 1948; Berland, 1961; Hansen, 1963) and Canada (Drainville, 1960; Coad, 1995). Once considered abundant in the fjords of south-east Greenland (Jensen, 1948), *S. microcephalus* has been caught to the innermost limit of multiple fjord basins (Jensen, 1948; Bjerkan, 1957; Drainville, 1960) possibly following annual migrations of native groundfishes (Bjerkan, 1957). Alternatively, fjords may also represent a pupping ground as the only *S. microcephalus* captured with near-term embryos were found near fjords in the Faeroe Islands (Bjerkan, 1957). Fish approaching the natal size estimates described above have been caught in fjords in Canada, Norway (Bjerkan, 1957), and Greenland (Jensen, 1948). There are insufficient data, however, to determine whether fjords represent important pupping areas (Heupel *et al.*, 2007).

The only active tracking study of *S. microcephalus* movement in the Arctic Ocean to date is from Victor Bay, Canada. Skomal & Benz (2004) acoustically tracked the small-scale vertical and horizontal movements of six fish under sea ice for short periods of time (<43 h), finding that the fish were not exclusively benthic, but rather exhibited substantial vertical movements. Similar results have been observed in Quebec, Canada where a single passively tracked animal was recorded both on the bottom and making diurnal migrations into the water column (Stokesbury *et al.*, 2005). Significant vertical movements observed in many shark species are thought to be associated with foraging (Sundström *et al.,* 2001). This behaviour was, however, reported to be unusual for an elasmobranch perceived to be a deep-water benthic predator. Other large, deep-water sharks have generally remained near the bottom when observed *in situ*. Carey & Clarke (1995) observed two sixgill sharks *Hexanchus griseus* (Bonnaterre 1788) near Bermuda that remained consistently near the bottom at depths of 600–1100 m and the deep-water needle dogfish *Centrophorus acus* Garman 1906 kept within 50 m of the 220–680 m deep seabed during a 21 h track off Japan (Yano & Tanaka 1986).

Skomal & Benz (2004) calculated average swimming speeds for *S. microcephalus* based on assumptions of straight-line movement and constant receiver range; their conservative estimate of 0·22 m s^{-1} was similar to that obtained by Yano & Tanaka (1986) for *C. acus* (0·25 m s^{-1} during the day). Although the range of speeds estimated for *S. microcephalus* overlapped somewhat with other sharks (Sundström *et al.*, 2001), they were much slower than those estimated for large predators like the white shark *Carcharodon carcharias* (L. 1758) (0·89 m s^{-1}, Carey *et al.*, 1982; Strong *et al.*, 1992) and tiger shark *Galeocerdo cuvier* (Péron & LeSueur 1822) (1·07 m s^{-1}, Lowe *et al.*, 1996; Holland *et al.*, 1999). *Somniosus microcephalus* tagged by Skomal & Benz (2004) displayed vertical rates of ascent (0·06 m s^{-1}) and descent (0·10 m s^{-1}) typical for a shark cruising in a search mode (Strong *et al.*, 1992). Skomal & Benz (2004) reported that *S. microcephalus* appeared to be near neutrally buoyant in the water column.

Conventional, satellite and acoustic tagging of *S. microcephalus* have provided evidence for both site fidelity and large-scale movements in excess of 1100 km (Hansen, 1963). From 1936 to 1949, Hansen (1963) tagged 411 fish off the western coast of Greenland. Of 28 tag recaptures made, six fish were caught within 16 km of the tagging site after 1–7 years. Seven fish travelled 16–160 km up to 14 years after tagging, while the remaining 17 travelled 160–1100 km after 2–16 years at liberty. The longest distance travelled over the shortest duration was 370 km in 2 years. Unfortunately, Hansen's (1963) recapture data were insufficient to discern temporal or spatial movement patterns. More recently, Stokesbury *et al.* (2005) placed satellite tags on two individuals, finding maximum movement of 115 km over 69 days. From these data it can be concluded that *S. microcephalus* can make large-scale (100–1000 km) movements throughout the year, however, much additional data are required to sufficiently characterize seasonal movements.

SIZE, GROWTH AND ABUNDANCE

Somniosus microcephalus is one of the largest shark species and is the largest fish inhabiting Arctic Ocean waters. While maximum size estimates of 756 cm L_T have been reported in the literature, the largest reliably measured *S. microcephalus* was total length (L_T) 640 cm L_T and total mass (M_T) 1023 kg (Bigelow & Schroeder, 1948). Most reported sizes have been between 288 and 504 cm (Bigelow & Schroeder 1953; Fisk *et al.*, 2002). Fish collected from Norway in 2008 ranged between L_T 245 and 389 cm (mean ± s.d. 301 ± 30 cm; $n = 32$; pers. obs.) while Yano *et al.* (2007) reported L_T ranges of between 65 and 480 cm (mean ± s.d. 274 ± 118 cm; $n = 38$).

On the basis of measurements of 120 specimens from Aberdeen, U.K., Bigelow & Schroeder (1948) observed that females were, on average, larger than males at 472 and 343 cm respectively, an observation supported by Yano *et al.* (2007). Since

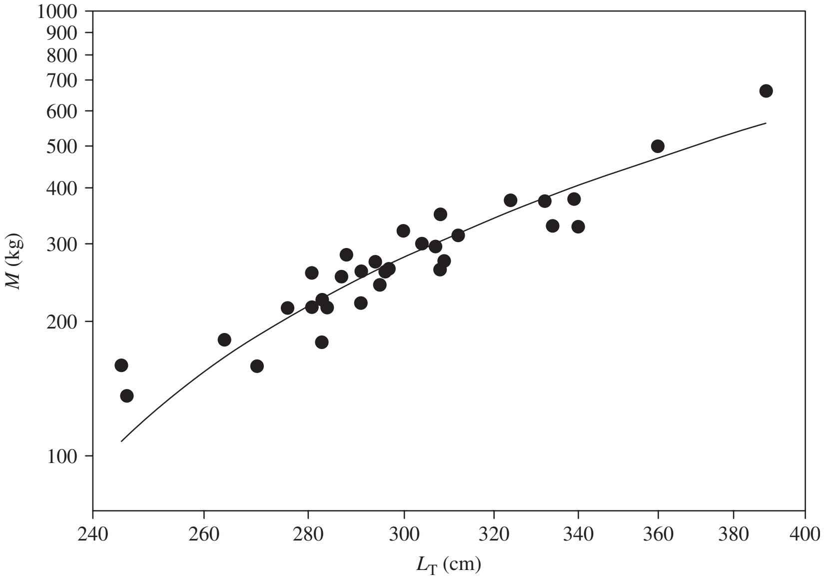

FIG. 5. The mass (M) relationship and total length [L_T, $\ln y = -12{\cdot}2\ (\pm 1{\cdot}1) + 3{\cdot}13\ (\pm 0{\cdot}20) \ln x$; $r^2 = 0{\cdot}89$, $n = 35$; values in parentheses are ± S.E.] for *Somniosus microcephalus* collected in June 2008 from Kongsfjorden, Svalbard. There was little evidence of differences between sexes, which were combined.

1998, specimens have been collected (pers. data) from across the known range of *S. microcephalus* including: Iceland (2001–2005), where L_T mean± S.D. were 345·0 ± 6·2 cm for males ($n = 3$) and 435·5 ± 34·2 cm for females ($n = 23$); the Canadian Arctic (1998–1999), where L_T mean± S.D. were 286 ± 5·8 cm for males ($n = 15$) and 282 ± 6·9 cm for females ($n = 10$); Svalbard (2008), where mean L_T were 293 ± 23 cm for males ($n = 13$) and 305 ± 34 cm for females ($n = 19$).

To date, no L_T and mass (M) relationships have been published for *S. microcephalus*, possibly due to its large size and the logisticical difficulties of working in the Arctic. In June 2008, the L_T and M of 32 (13 male and 19 female) *S. microcephalus* caught from Kongsfjorden, Svalbard (78° 58′ N; 11° 51′ E) were collected (pers. data). From these limited data, weak evidence for sex-related differences in the L_T–M relationship (male: $a = 0{\cdot}0000004$ and $b = 3{\cdot}57$; female: $a = 0{\cdot}000014$ and $b = 2{\cdot}94$) using a standard log-linear model ($\ln M = \ln a + b \ln L_T$) (Wigley *et al*., 2003) was observed. With both sexes modelled together the M (kg) and L_T (cm) relationship was derived (Fig. 5). These parameter estimates ($a = 0{\cdot}000005$ and $b = 3{\cdot}13$) fall within the mid-95% C.I. range for North Atlantic fish [$a = 0{\cdot}00002$ (0·0000007–0·000122), $b = 3{\cdot}02$ (2·53–3·52); E. Cortés, unpubl. data].

Unlike many shark species, age estimates for *S. microcephalus* have not been calculated because conventional vertebral ageing methods are not possible; *S. microcephalus* vertebrae contain homogenous cartilage, with no apparent calcification into distinct bands. Limited growth rate data from the tag–recapture studies of Hansen (1963) suggested a life span in excess of 100 years, however, only a single fish was reliably measured at both tagging and upon recapture. This individual was at liberty for 16 years and had grown from 262 to 270 cm, an average of 0·5 cm year^{-1}

(Hansen, 1963). Given the slower metabolic rates observed among polar fishes (Clarke & Johnston, 1999) and an estimated 40–100 cm size at birth (Koefoed, 1957; Kondyurin & Myagkov, 1983), 600 cm individuals may be among the oldest of any fish species.

No population assessments have been attempted for *S. microcephalus,* but earlier commercial shark-liver oil fisheries in Davis Strait and Baffin Bay, Canada, and Norwegian and Greenland Seas provide some insight into their abundance. The largest catches on record were in the 1940s when, at the height of the fishery, an estimated 50 000 animals were landed from the waters of both western and eastern Greenland (Jensen, 1948). *Somniosus microcephalus* are also commonly observed in the upper North Atlantic and eastern Arctic Oceans by researchers, fishers and sealers, who have anecdotally reported hundreds of individuals in a single season (Jensen, 1948; Dunbar & Hildebrand, 1952; Templeman, 1963). Exploratory fishing has thus far resulted in >2 fish 100 hooks^{-1} in Cumberland Sound, using gear for flat-fish; >15 fish 100 hooks^{-1} and >20 fish 100 hooks^{-1} have been caught in Cumberland Sound and Svalbard, respectively, using gear designed for sharks (unpubl. data).

DIET AND TROPHIC STATUS

On the basis of the wide variety of invertebrates, fishes and marine mammals that are found in their stomachs, *S. microcephalus* is a generalist feeder of both benthic and pelagic organisms (Bigelow & Schroeder, 1948; Jensen, 1948; Dunbar & Hildebrand, 1952; Williamson, 1963; Beck & Mansfield, 1969; Ridoux *et al*., 1998; Fisk *et al*., 2002; McMeans *et al.,* 2010; LeClerc 2011; LeClerc *et al.,* 2011).

Fishes are the most common dietary item (by mass and numbers of individuals) found in the stomachs of *S. microcephalus* collected across a range from the Canadian Arctic to Iceland, northern Scotland and Svalbard (Bigelow & Schroeder, 1948; Jensen, 1948; Dunbar & Hildebrand, 1952; Williamson, 1963; Beck & Mansfield, 1969; Fisk *et al*., 2002; McMeans *et al.,* 2010; LeClerc, 2011). *Somniosus microcephalus* from the Canadian Arctic have been reported to eat herring *Clupea harengus* L. 1758, Atlantic salmon *Salmo salar* L. 1758, *S. alpinus*, capelin *Mallotus villosus* (Müller 1776), *R. hippoglossoides*, thorny skate *Amblyraja radiata* (Donovan 1808) and other flatfishes (Coad 1995; Fisk *et al*., 2002). Redfish *Sebastes Sebastes viviparus* Krøyer 1845 L. 1758 dominated the fish contents found in the stomachs of many Iceland-caught *S. microcephalus* (McMeans *et al.,* 2010), but a range of other species have also been found.

Invertebrates are also found in *S. microcephalus* stomachs; squid, snails, pelecypods, crabs, mudstars, brittle stars and jellyfish have been reported from northern Atlantic and Canadian Arctic waters (Coad 1995; Fisk *et al*., 2002), although not in fish collected around Iceland and Svalbard (McMeans *et al., 2*010; LeClerc, 2011). Several species of Lysianassidae amphipods (*e.g. Anonyx nugax* and *Orchomenella pinguis*) that feed on dead animal tissue have been found in *S. microcephalus* stomachs sampled in Cumberland Sound, indicating recent scavenging events (unpubl. data).

Marine mammal tissue has been repeatedly observed in *S. microcephalus* stomachs (Bigelow & Schroeder, 1948; Jensen, 1948; Dunbar & Hildebrand, 1952; Williamson, 1963; Beck & Mansfield, 1969; Ridoux *et al*., 1998; Fisk *et al*., 2002; McMeans *et al.,* 2010; LeClerc 2011) with pinnipeds being most frequently reported where identification could be made. Ridoux *et al.* (1998) and Fisk *et al.* (2002) found young ringed seals *Pusa hispida* in the stomachs of *S. microcephalus* off the coast of Iceland and in Cumberland Sound. Fisk *et al.* (2002) also reported the tissue of an unidentified marine mammal in a *S. microcephalus* stomach that, based on the experience of a local Inuit hunter and fisherman (D. Evic, pers. comm.) and the length of the muscle fibres found, was thought to be beluga whale *Delphinapterus leucas*, narwhal *Monodon monoceros*, or walrus *Odobenus rosmarus*. Two *S. microcephalus* captured in Baffin Bay in September 1999 contained the bodies of two headless juvenile seals: harp seal *Phoca groenlandica* [Fig. 6(a)] and *P. hispida*, flippers of an adult seal, and an *c*. 0·3 × 1·0 m piece of skin and blubber. Of 23 *S. microcephalus* in Iceland with stomach contents, eight contained marine mammals including an unknown sample, two pinniped pieces, two juvenile porpoises, and a section of *U. maritimus* [Fig. 6(b)] (unpubl. data). Although the evidence is clear that marine mammals are a frequent component of *S. microcephalus* diet, it remains unknown whether these represent scavenging events or active feeding [Fig. 6(c)]. *Somniosus microcephalus* clearly scavenge, as minke whale *Balaenoptera acutorostrata* harvested by Norway were genetically identified in *S. microcephalus* stomachs (LeClerc *et al.,* 2011). Yet over-wintering *D. leucas* that must continually swim to keep breathing areas of open water through annual sea ice, have also been observed with large, circular bites in their skin that correspond to the gape size of *S. microcephalus* [Fig. 4(d)] (pers. obs.); no other Arctic species is known that could inflict such wounds. It would appear therefore that over-wintering whales face not only surface threats from *U. maritimus*, but also sub-surface threats from *S. microcephalus* that, despite their limited vision, may actively feed at ice-holes.

The *S. microcephalus* diet includes both benthic and pelagic prey, although the relative importance of benthic prey appears to vary across their range. A greater proportion of pelagic fishes were found in fish stomachs from Iceland *v*. those from the Canadian Arctic although this may reflect differences in collection methods (gillnets and trawls in Iceland *v*. bottom longlines in the Canadian Arctic) or L_T (Iceland: mean ± S.E. 416 ± 25; Canadian Arctic: 284 ± 4·4 cm; Fisk *et al*., 2002; McMeans *et al.,* 2010). Often, a single fish will contain both benthic and pelagic species in its stomach, consistent with the diurnal behaviour of *S. microcephalus* reported by Skomal and Benz (2004). The feeding behaviour of this fish in more temperate waters is unknown.

Stable isotopes of nitrogen (δ^{15}N) and carbon (δ^{13}C), OCs, and Hg have also been used, in combination with stomach contents, to assess the relative trophic position and carbon sources of *S. microcephalus* collected in Cumberland Sound (Fisk *et al*., 2002) and the waters surrounding Iceland (McMeans *et al.,* 2010). These tracers can overcome a number of problems associated with stomach contents such as different rates of digestion of prey items, unidentified material, and limited sample size (Hyslop, 1980; Pinnegar & Polunin, 2000), and provide a longer-term averaged assessment of feeding. Tracer data provides an additional tool with which to assess diet, that is particularly useful for *S. microcephalus* given their cold-water distribution, the limited availability of stomach-content data, and the wide range of items found in their stomachs.

Values of δ^{15}N, which provide a metric of relative trophic position (Vander Zanden & Rassmussen, 2001), for *S. microcephalus* and potential prey items have suggested

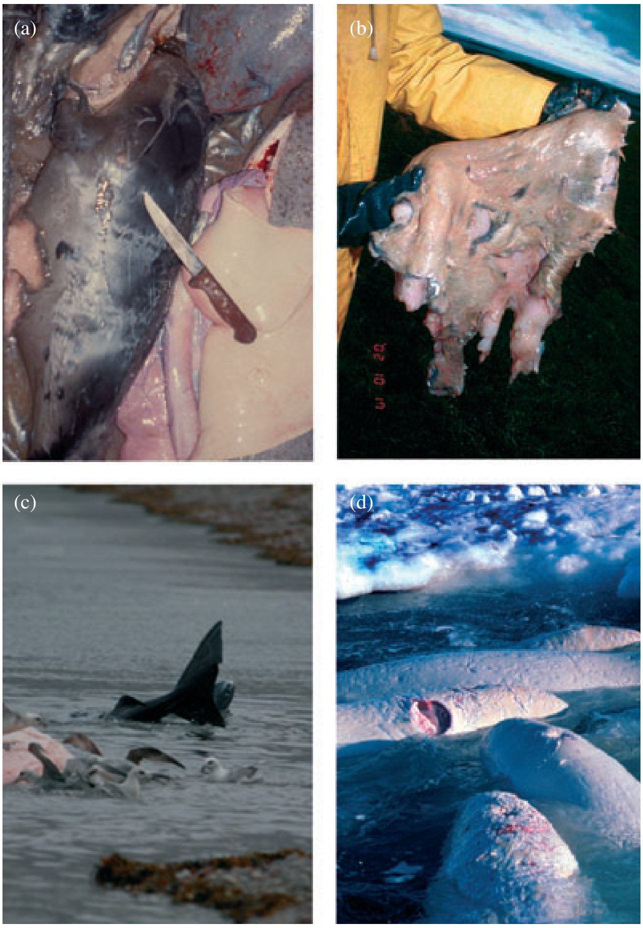

FIG. 6. (a) Pagophillus groenlandicus pup and (b) *Ursus maritimus* skin from *Somniosus microcephalus* stomach; (c) *Somniosus. microcephalus* feeding on *Monodon monoceros* carrion in Repluse Bay, Nunavut, Canada, (d) *Delphinapterus leucas* possibly showing *S. microcephalus* wounds.

a trophic position of *c*. 4 in Cumberland Sound and Iceland (Fisk *et al*., 2002; McMeans *et al.,* 2010), based on the common diet-tissue discrimination factor of 3·8‰ used for Arctic food-web studies (Hobson *et al*., 2002). This is in agreement with the conclusions of Cortés (1999) who estimated a trophic position of 4·2 based on the stomach content data from a single study. This would place the fish at the same trophic position as *P. hispida* in Cumberland Sound and common porpoise *Phocoena phocoena* in Iceland, although both of these species have been found in *S. microcephalus* stomachs. *Somniosus microcephalus* OC (*e.g.* PCBs and DDT) and Hg concentrations, contaminants that biomagnify through Arctic food webs (Fisk *et al.,* 2001; Campbell *et al.,* 2005) were similar to *L. hyperboreus* and *U. maritimus* from the Canadian Arctic (isotope-derived trophic levels of 4·6 and 5·5 respectively; Hobson *et al*., 2002), indicating that at times *S. microcephalus* may be a fifth trophic position predator. Elevated levels of the chlordane metabolite oxychlordane, a compound that is not formed efficiently in fishes, are consistent with these results, most probably accumulating through the consumption of marine mammals (Fisk *et al.*, 2002). As well, a recent study using large, aquarium-held sharks found that diet-tissue discrimination factors for δ^{15}N should only be 2·3‰ for muscle (Hussey *et al.,* 2010). Using this value, estimates of trophic position of *S. microcephalus* using δ^{15}N would be closer to 5.

Values of δ^{13}C indicate that the carbon sources in *S. microcephalus* diets of Cumberland Sound and Iceland are derived from a combination of benthic and pelagic sources (Fisk *et al.*, 2002; McMeans *et al.*, 2010) which is consistent with observed stomach contents. Pelagic primary productivity has relatively depleted (more negative) values of δ^{13}C than benthic production, allowing the relative importance of these sources to be established (France, 1995; Hobson *et al.*, 2002). High trophic level organisms in aquatic systems have demonstrated δ^{13}C values that are intermediate between benthic and pelagic values due to integration of different carbon sources (Hecky & Hesslein, 1995) and thus, the intermediate δ^{13}C signal seen in some *S. microcephalus* may be partially due to a high trophic position, consistent with δ^{15}N values.

FISHERIES AND THREATS

Fishing for *S. microcephalus* has been a part of Scandinavian, Inuit and Icelandic cultures for centuries. The earliest catch records date to the 14th Century in Iceland and the 13th Century in Norway, mostly in association with fisheries for cod *Gadus morhua* L. 1758 using sprawl-lines, longlines or hand-lines set between 35 and 365 m (Kristjánsson, 1983). A shark-specific sprawl-line, consisting of surface floats and a sink with hooks attached to a line set close to the bottom, appeared as a directed fishery in Iceland during the early 1600s and was commonly used well into the 19th Century; however, hand lines were the most common gear used in the region to fish for *S. microcephalus*. Traditional shark fishing vessels were often small (5·6–6·3 m), open rowboats, with six to eight fishermen present, although larger (7·5 m) ten-man boats were also used (Kristjánsson, 1982, 1983). Around 1820, the Icelandic shark fishery began to use larger, closed-deck vessels for periods of up to 7 days with each boat landing up to 13 animals per cruise (Thor, 2002).

Shark liver oil was sold to continental Europe for several hundred years and the earliest records, from 1624, show 930 barrels (111 600 l) of oil were exported in that year; subsequent export volumes ranged from 244 to 1742 barrels per year (Jónsson 1994). The 17th and 18th Centuries saw expansions in the shark fishery due to increased liver oil demands from Europe. The export market grew from 2025 barrels in 1819 to a peak of 13 000 barrels in 1867. From *c*. 1860 until the mid 1900s, *S. microcephalus* was harvested extensively on baited hook and line in Greenland as a valuable source of lamp fuel (Jensen, 1914, 1948; Clark, 1915). The demand for export shark liver oil decreased early in the 20th Century and, although fishing continued around Greenland until 1948, Icelandic export ended around 1930. One-and-a-half barrels of raw liver were needed to produce one barrel of smelted oil for export (Kristjánsson, 1983). A medium sized (*c*. 4·2 m) female *S. microcephalus* liver is *c*. 50 kg (or 50 l), and each barrel contained 120 l of oil. An estimated 47 000 fish were processed in the 1867 oil export market and the annual catch remained between 1200 and 38 500 fish from 1868 to 1900.

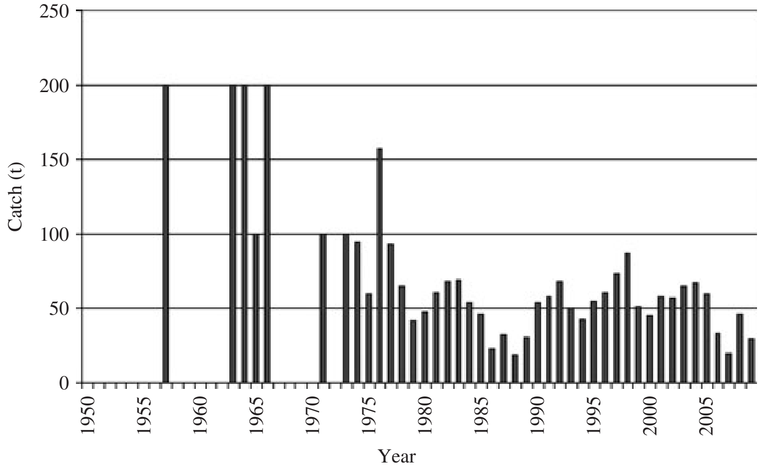

FIG. 7. FAO *Somniosus microcephalus* catch statistics, 1957–2009. (FAO, 2011).

In Norway, peak annual catches occurred in 1948 with nearly 2·8 million kg of shark liver oil corresponding to *c*. 58 000 individuals. Iceland remains one of the few countries where *S. microcephalus* is still targeted in a directed fishery, mostly due to its use in the Icelandic delicacy *hákarl*. Shark tissues have also been used to make knives, bookbinding, and dog food throughout Greenland and the eastern Canadian Arctic (Jensen, 1948; McAllister, 1968; Coad, 1995) although no large-scale market for *S. microcephalus* meat has developed to date.

The Food and Agricultural Organization (FAO) of the United Nations began keeping data on *S. microcephalus* in 1957 in their Global Capture Production database that compiles reports of landed catch from regional fisheries management organizations and individual countries. Catches reached a maximum of 200 t around 1960 and have fallen to near 50 t since the early 1980s (Fig. 7). German fisheries maintained the highest catches from 1963 to 1966 and Icelandic fisheries have caught the most fish from the early 1970s to the present (FAO, 2011). Much of the catch of *S. microcephalus,* however, is considered by-catch and would not be reported to FAO.

Somniosus microcephalus is a common by-catch species in both the *R. hippoglossoides* and northern shrimp *Pandalus borealis* fisheries in the north-west Atlantic Ocean. Data from Fisheries and Oceans Canada (DFO) observer programmes in Atlantic Canada show by-catch of *S. microcephalus* increased from relatively low levels in the 1980s to *c*. 800 t from 1990 to 1993. This marked increase was comprised mainly of catches from Northwest Atlantic Fisheries Organization (NAFO) Subarea 0 (Baffin Bay and Davis Strait) and Subarea 2 (Labrador Sea; Fig. 8; see www.nafo.ca for a description of NAFO fishing areas) and corresponds with a significant increase in fishing effort directed towards *R. hippoglossoides* in these areas (Bowering & Brodie 1994). By-catch declined during the late 1990s, but began to increase again in 2000, corresponding with increased effort in the *R. hippoglossoides* fishery in the northern portion of Subarea 0 (Treble & Bowering, 2002). Between 2002 and 2008 by-catch fluctuated between 100 and 200 t and in recent years has declined to just below 100 t (Fig. 8). While observers are mandatory on large offshore factory freezer ships, smaller (20 to 30 m) vessels are inconsistently monitored,

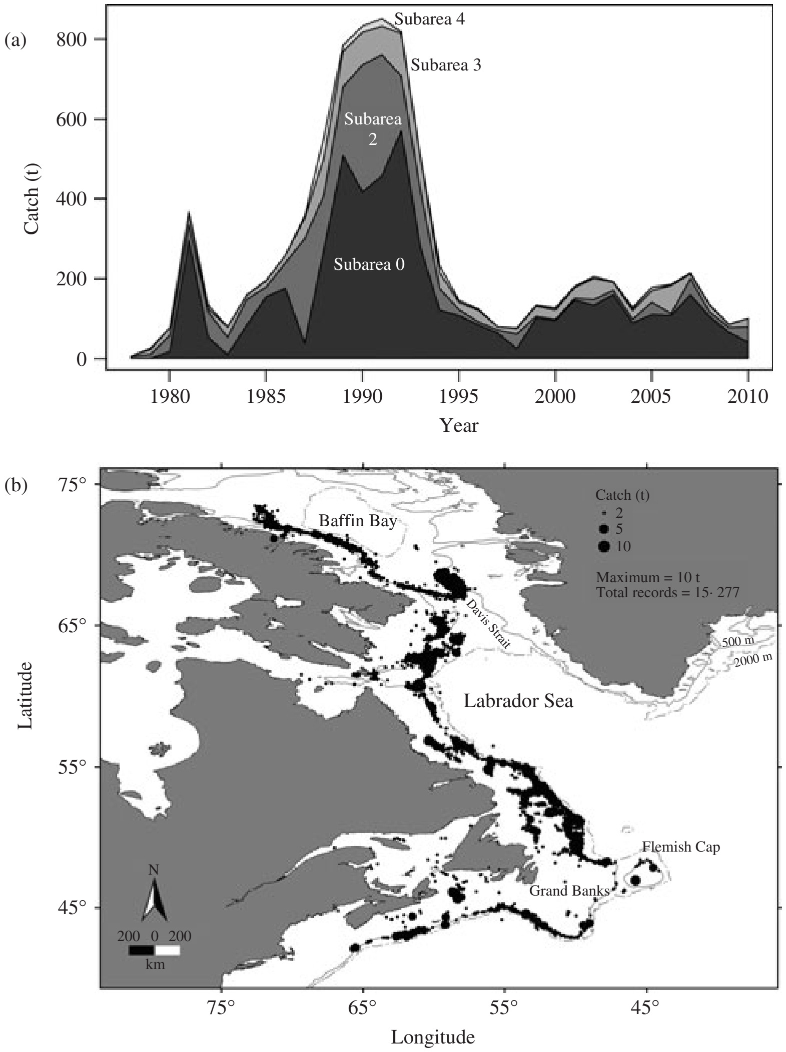

FIG. 8. (a) *Somniosus microcephalus* by-catch for NAFO fishery statistic subareas by year and (b) location as reported by onboard observers deployed by Fisheries and Oceans Canada (1978–2010).

therefore, these estimates of *S. microcephalus* by-catch are underestimated. There is also the possibility that some of the catches are misidentified basking shark *Cetorhinus maximus* (Gunnerus 1765), particularly in waters south of 51° N latitude where *C. maximus* are most abundant (NAFO Subareas 3 and 4; COSEWIC, 2009; J. Firth & M. Simpson, pers. comm.). Onboard observers report that some *S. microcephalus* caught in offshore trawl and longline fisheries are released alive and in reasonably good condition, although no survivorship estimates are currently available.

Somniosus microcephalus have also been reported as by-catch in Spanish fisheries for *R. hippoglossoides* in NAFO Subarea 3 (Grand Banks and Flemish Cap). For the period 1991 to 1999 *S. microcephalus* contributed from 0·2 to 2·1% of the total catch by mass, of all species in the Spanish fleet (Durán *et al*., 1999; P. S. Durán &

TABLE I. *Somniosus microcephalus* by-catch, total number of sets reported, catch per set and the number of fishermen, and *Reinhardtius hippoglossoides* catch for the Cumberland Sound winter fishery, 1987–2006 and summer fishery 2009

Year	Catch (numbers)	Long-line sets (numbers reported)	Shark mean (catch per set)	Number of fishermen*	*R. hippoglossoides* (t)
1987	15	111	0·14	na (6)	4
1989	121	824	0·15	na (43)	180
1990	80	1428	0·06	na (77)	255
1991	52	1317	0·04	45 (61)	139
1992	26	498	0·05	na (93)	430
1993	28	496	0·06	na (115)	425
1994	61	717	0·09	na (107)	402
1995	220	1782	0·12	23 (97)	285
1996	29	221	0·13	5 (30)	61
1997	186	1148	0·16	12 (15)	66
1998	172	601	0·29	4 (na)	63
1999	104	596	0·17	5 (12)	34
2000	137	710	0·19	7 (13)	45
2001	17	208	0·08	2 (15)	78
2002	60	705	0·12	5 (30)	106
2003	24	528	0·05	4 (35)	242
2006	4	74	0·05	1 (10)	70
2009†	570	68	8·38	1 vessel	35·3

*Number of fishermen who completed logbooks and (total number participating in the fishery).
†Summer fishery.

X. Paz. Junquera, unpubl. data). Prior to 1994, catches of *S. microcephalus* in the Spanish fishery varied between 55 and 69 t and then increased to between 107 and 434 t. The increase was probably due to heightened fishing effort by the Spanish fleet, as no other changes in the fishery, such as depths or locations, occurred (P. S. Durán, pers. comm.).

In Cumberland Sound there has been a relatively small long-line fishery for *R. hippoglossoides* that has been conducted exclusively in winter through the ice from 1987 until 2009, when it expanded to include a summer fishery. *Somniosus microcephalus* is one of the main by-catch species in this fishery (DFO, 2008; Idrobo, 2008; Young, 2010). For the winter fishery, fishermen are asked to voluntarily record their catches in logbooks, providing a minimum estimate of *S. microcephalus* catch; by-catch of *S. microcephalus* has varied between 15 and 220 animals (Table I). For the developing summer fishery, by-catch of *S. microcephalus* can be considerably higher (500 fish or more; Table I). In both fisheries, fish that are badly tangled in the longline gear are often killed by removing the tailfin to avoid having to cut and splice the main fishing line (Idrobo, 2008).

Recreational catch and release fisheries have developed for *S. microcephalus* in Norway, where it is caught year-round, and in Greenland, where it is caught through the sea ice in March.

CONCLUSIONS

Much of what is currently known about *S. microcephalus* has been as a result of incidental by-catch, observations in deep-water fisheries, and from a limited pool of directed studies. Yet the combination of available stomach contents, stable isotopes and contaminant concentrations suggest that the fish is a high trophic position predator and, if *S. microcephalus* continues to inhabit Arctic basins in accordance with their historic abundance, these limited data suggest that this fish may play a substantial role in the trophic dynamics of Arctic marine ecosystems. Because Arctic waters have few species occupying a limited number of functional roles (Chapin *et al.*, 1997), *S. microcephalus* may become an important top-down consumer as the role of better-known predators such as *U. maritimus* is diminished (Derocher *et al.*, 2004). Similar to many shark species, the limited understanding of *S. microcephalus'* current and potential trophic role is an important gap in knowledge about this animal.

Despite these gaps, it is clear that *S. microcephalus* are, for such a large fish, relatively abundant in the Arctic and upper North Atlantic Ocean basins. It is a species that experiences little apparent fishing pressure beyond incidental by-catch and there is no indication that it is under conservation stress. It may be that the isolation of the Arctic region and the low-levels of fishing there have protected the species to date. The Arctic may, however, soon experience substantial fishing pressures following the demise of multi-year sea-ice, the seasonal retraction of annual ice cover, and the northward migration of commercial fish stocks. The slow-growing life-history of *S. microcephalus* may yet make it vulnerable.

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