Polar Biol
DOI 10.1007/s00300-014-1610-y

ORIGINAL PAPER

Juvenile Greenland sharks *Somniosus microcephalus* (Bloch & Schneider, 1801) in the Canadian Arctic

Nigel E. Hussey · Aurelie Cosandey-Godin · Ryan P. Walter · Kevin J. Hedges · Melanie VanGerwen-Toyne · Amanda N. Barkley · Steven T. Kessel · Aaron T. Fisk

Received: 11 March 2014 / Revised: 19 October 2014 / Accepted: 28 October 2014

Abstract Life-stage-based management of marine fishes requires information on juvenile habitat preferences to ensure sustainable population demographics. This is especially important in the Arctic region given very little is known about the life histories of many native species, yet exploitation by developing commercial and artisanal fisheries is increasing as the ice extent decreases. Through scientific surveys and bycatch data from gillnet fisheries, we document captures of rarely reported juvenile Greenland sharks (*Somniosus microcephalus*; ≤200 cm total length [TL]) during the ice-free period in the Canadian Arctic. A total of 22 juvenile animals (42 % of total catch; $n = 54$), including the smallest reliably measured individual of 117 cm TL, were caught on scientific longlines and bottom trawls in Scott Inlet and Sam Ford Trough over three consecutive years. Molecular genetic nuclear markers confirmed species identity for 44 of these sharks sampled; however, two sharks including a juvenile of 150 cm TL were identified as carrying a Pacific sleeper shark (*Somniosus pacificus*) mitochondrial cytochrome *b* (cyt *b*) haplotype. This represents the first record of a Pacific sleeper shark genetic signature in Greenland sharks in Eastern Arctic waters. Juvenile sharks caught as bycatch in gillnet fisheries were only observed offshore in Baffin Bay surrounding a fishery closure area, while larger subadult and mature Greenland sharks (>200 cm TL) were caught in all fishing locations, including areas where juveniles were observed. The repeatable occurrence of juvenile Greenland sharks in a fjord and their presence at two offshore sites indicates that these smaller animals either reside in nurseries or have defined home ranges in both coastal and offshore regions or undertake large-scale inshore–offshore movements.

Keywords Greenland shark · Pacific sleeper shark · Nursery grounds · Juvenile sharks · Genetics · Scott Inlet · Sam Ford Trough · Baffin Bay

Introduction

Understanding the habitat preferences of a species across life stages is a critical aspect for both species- and ecosystem-based management. For marine fishes, life-stage-based management typically breaks species movements and habitat preferences into discrete size-based components centered on maturity states, i.e., juvenile, subadult and mature adult stages. Young-of-year and juveniles are an important size component, as these individuals form new cohorts that structure the future demography of a stock (Beck et al. 2001; Heupel et al. 2007) and ultimately dictate sustainable quotas for directed fisheries as well as acceptable levels of bycatch. For marine elasmobranchs that are typically k-selected and prone to over-exploitation (Dulvy et al. 2014), defining birthing habitat and identifying essential fish habitat of juvenile animals is consequently a priority.

N. E. Hussey (✉) · R. P. Walter · A. N. Barkley · S. T. Kessel · A. T. Fisk
Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4, Canada
e-mail: nehussey@uwindsor.ca

A. Cosandey-Godin
Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada

A. Cosandey-Godin
WWF-Canada, Halifax, NS B3J 1P3, Canada

K. J. Hedges · M. VanGerwen-Toyne
Arctic Aquatic Research Division, Fisheries and Oceans Canada, Winnipeg, MB R3T 2N6, Canada

Published online: 06 November 2014

Pupping grounds and juvenile habitat for many elasmobranch species is commonly categorized as either coastal or offshore (Heupel et al. 2007). Species such as the blacktip (*Carcharhinus limbatus*) and sandbar (*Carcharhinus plumbeus*) shark deliver young in coastal environments (bays or semi-enclosed shallow water systems) where the juveniles remain resident in discrete nursery grounds, for a period of months to years, prior to undertaking larger-scale movements (Heupel and Hueter 2002; Conrath and Musick 2007; DeAngelis et al. 2008; Conrath and Musick 2010). This strategy is considered to have evolved to partition habitats between young and adults/large predators to minimize juvenile population mortality (Morrissey and Gruber 1993a; Heupel and Simpfendorfer 2002; Dibattista et al. 2007). For pelagic species such as the blue (*Prionace glauca*) and silky (*Cacharhinus falciformis*) shark, juvenile habitat is less well defined and young are birthed offshore (Driggers et al. 2008; Montealegre-Quijano and Vooren 2010). Young are often born at a larger size and litter size is larger (Cortés 2000); selective mechanisms thought to balance high rates of expected mortality (but see slow-reproducing sharks; Tsai et al. 2010; Semba et al. 2011). Many elasmobranch species are also thought to be philopatric and return to the same nursery grounds where they were born as mature adults to birth (Hueter et al. 2004; Feldheim et al. 2014). Habitat variability among juvenile elasmobranchs therefore imparts differential consequences for management.

The Greenland shark (*Somniosus microcephalus*), an Arctic-boreal species (Lynghammar et al. 2013), is one of few elasmobranchs that occurs in Arctic waters and is one of the largest carnivorous shark species, reaching a maximum size of ~6 m total length (TL) (MacNeil et al. 2012). Although emerging work is starting to reveal the diet (Leclerc et al. 2012; Nielsen et al. 2014), ecological role (Fisk et al. 2002; McMeans et al. 2013; Hussey et al. 2014), movements (Skomal and Benz 2004; Fisk et al. 2012; Campana et al. 2014) and contaminant dynamics (McKinney et al. 2012) of this species, aspects of its biology and ecology remain poorly understood. Although the age of Greenland sharks is unknown, preliminary growth rates of <1 cm per year (Hansen 1963) suggest that the species is long-lived and potentially one of the oldest elasmobranchs, ranking the Greenland shark as a high-risk species in terms of fisheries exploitation and bycatch (see review by MacNeil et al. 2012 and references therein). Historically, the Greenland shark was subjected to high levels of exploitation (Jensen 1914, 1948; FAO 2014), but currently there are no data to assess the state of the stock. With decreasing ice cover extent and the expansion of fisheries in the Arctic (Christiansen et al. 2014), there is concern that this species could become overexploited as bycatch in commercial and artisanal fisheries. A proactive approach to Greenland shark management is therefore being advocated (Davis et al. 2013), but data on residency, movement patterns and essential habitats of this species are required particularly for juvenile and reproductively mature size classes.

The Greenland shark is considered a viviparous species (MacNeil et al. 2012), but to date, only one pregnant female containing 10 pups has been scientifically confirmed (caught offshore from the Faroe Islands with one pup examined; Koefoed 1957). A second suspected pregnant female was caught off Daviknes, Nordfjord, and contained a 98-cm fetus, but species identification is uncertain (Bjerkan 1944). The size of these reported in utero pups ($n = 2$; 37 and 98 cm) and the smallest free-swimming individuals (41.8-, 45.0-, 46.7-, 64.8- and two 100-cm TL individuals; Bigelow and Schroeder 1948; Kondyurin and Myagkov 1983; Kukuev and Trunov 2002; Yano et al. 2007) suggests a variable size at birth of ~40–100 cm TL. For the Pacific sleeper shark (*Somniosus pacificus*) a closely related cold-water species, variable birth size has also been documented [41.7 cm TL with a 15-mm umbilical scar (Francis et al. 1988) and 74 cm TL with a 1-mm umbilical scar (Ebert et al. 1987)]. Captures of juvenile free-swimming Greenland sharks (≤200 cm TL) are rare in the literature, and these size classes have not been encountered in research fishing activities in the Canadian Arctic over the past 15 years (Fisk and Hussey, pers. obs). The whereabouts and life history (coastal vs. offshore habitat) of juvenile Greenland sharks are therefore unknown and remain a major knowledge gap.

Here, we report data on the capture of juvenile Greenland sharks in Scott Inlet/Sam Ford Trough, Baffin Island, Nunavut, over three consecutive years and bycatch records of juvenile Greenland sharks caught in commercial Greenland halibut (*Reinhardtius hippoglossoides*) gillnet fisheries in Baffin Bay between 2008 and 2011. Species identification in Scott Inlet/Sam Ford Trough was confirmed by molecular genetic analysis given the difficulty of visually identifying *Somniosus* spp. in the field (Benz et al. 2007). These data provide the first description of potential juvenile Greenland shark habitat in the Canadian Arctic and summarize the geographical occurrences of small Greenland sharks across the Arctic region.

Methods

Sampling via scientific surveys: bottom longlines and bottom trawls

Bottom longlines were set within the narrow fjords of Scott Inlet and Sam Ford Trough, northeast Baffin Island, during research cruises on September 6, 2011, September 24/25, 2012, and September 18, 19, 24, 28 and 29, 2013 (Figs. 1, 2).

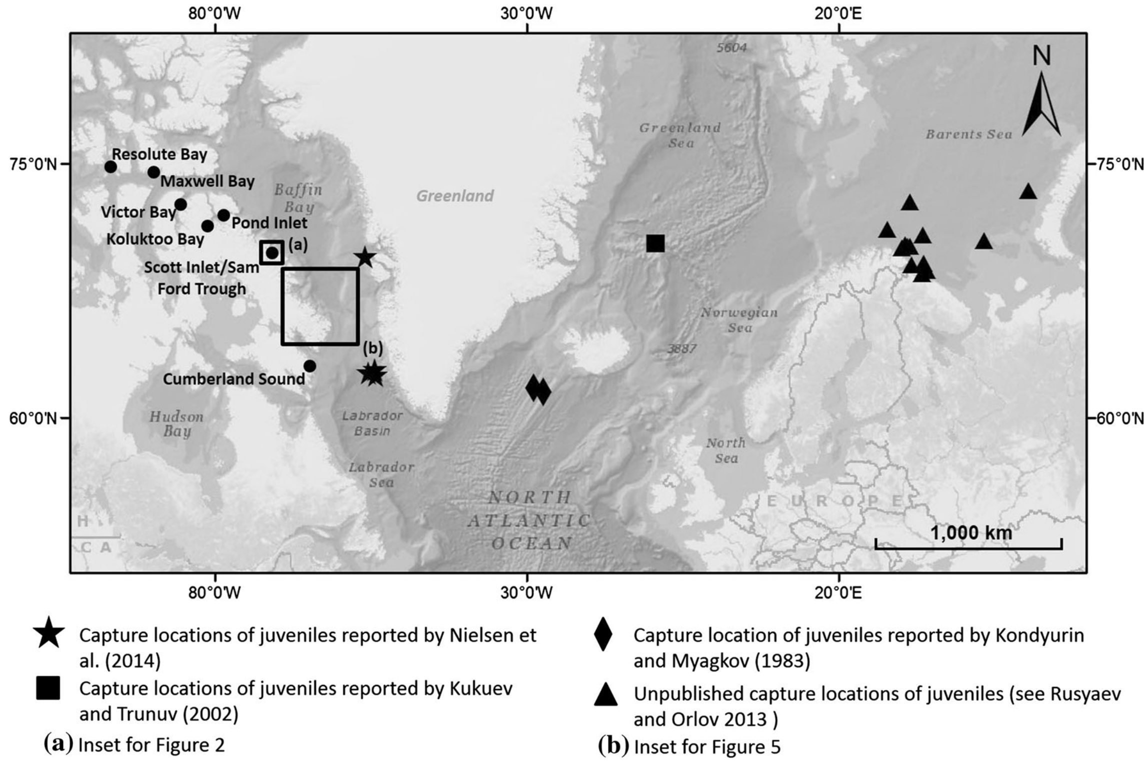

Fig. 1 Map of the North Atlantic and Arctic Ocean including **a** the study site of Scott Inlet and Sam Ford Trough and **b** the location of the offshore gillnet fishery for Greenland halibut (*Reinhardtius hippoglossoides*) in which Greenland sharks (*Somniosus microcephalus*) are caught as bycatch. Locations of previously reported captures of juvenile Greenland sharks across the Arctic region are marked

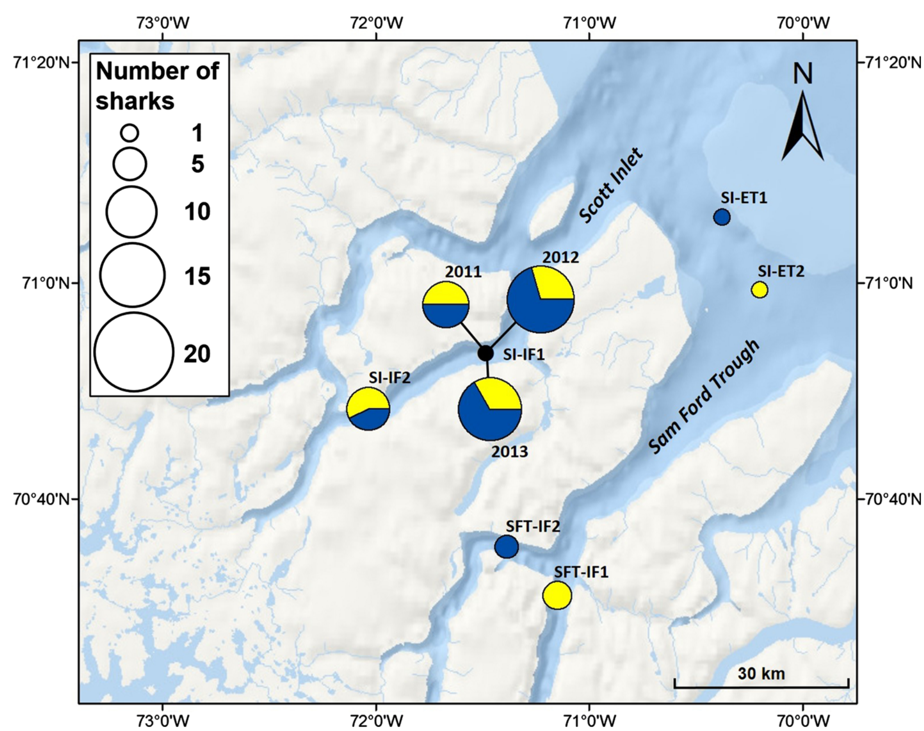

Fig. 2 Map of Scott Inlet/Sam Ford Trough with each circle marking the location where Greenland sharks (*Somniosus microcephalus*) were caught. *Yellow* (*light gray*) within a *circle* denotes the proportion of sharks caught at that site that were juveniles (≤200 cm TL), while *blue* (*medium gray*) denotes the proportion of subadult/adult sharks (>200 cm TL). The size of the *circle* is relative to the total number of sharks caught at that location. (Color figure online)

During all years, a standard baseline rope (9.2 mm diameter tarred black sinking line) was used ranging in length from 368 to 735 m. Gangions were either 0.9-m-long nylon thread with size 14 Mustad Duratin Tuna circle hooks (O. Mustad and Sons®) or 1.5-m steel leader with size 16 and 18 Mustad circle hooks spaced at 0.9 and 5.5 m, respectively. In

2011, bottom longline sets consisted solely of nylon gangions ($n = 400$ per set), in 2012, a mixture of nylon ($n = 400$) and steel leader ($n = 50$) and in 2013 only steel leader ($n = 50$). In total, eight successful longline sets were completed over 3 years (one in 2011, two in 2012 and five in 2013). Across all years, all hooks were baited with frozen squid. Bottom longlines were set in the early evening (approximately 20:00 h) and soaked for approximately 10–12 h. All bottom longlines were set in 668–800 m of water.

All sharks caught on longlines were secured by looping ropes around the caudal fin and across the pectoral fins; individuals were then dehooked, and if required, the caudal fin was disentangled from the baseline. The sharks were then held next to a zodiac and measured (total length [TL]—tip of snout to point of upper caudal lobe), sexed (presence or absence of claspers) and marked with an external dart tag (National Marine Fisheries Service Cooperative Shark Tagging Program). Prior to release, a small fin clip was taken from the pelvic or trailing edge of the dorsal fin for genetic analyses. In 2011, sharks were released directly from the line; consequently, TL was estimated by onboard scientists using landmarks on the side of the ship's hull and no fin clips were taken.

In addition to longlines, bottom trawls were conducted during 2013 to survey benthic biota and sharks were captured at this time. Bottom trawling was conducted using a Yankee style research trawl (~1,463 m of 1.43-cm-diameter cable on each drum). During each set, the trawl was fished in a straight line at a speed of ~3 knots for 30 min. Between September 17 and 29, 2013, nineteen trawl sets were conducted at the entrances of Scott Inlet/Sam Ford Trough at depths between 200 and 900 m. During bottom trawling, all sharks caught were brought onto the deck, processed as detailed above and released. Shark processing times 'in water' and 'on deck' were <20 min.

Genetic analysis

Both mitochondrial (mtDNA) and nuclear genetic analyses were performed on fin clips sampled from above captured sharks. We sequenced 702 bp of the mtDNA gene cytochrome *b* (cyt *b*) for each individual and compared these sequences with those previously reported by Murray et al. (2008). Genomic DNA was recovered from tissue samples using the Wizard Extraction kit (Promega), and cyt *b* was PCR amplified using the *Somniosus*-specific primers *Somn-GLU-L1* GAACCATCGTTGTTTATTCAAC and *Somn-CYTB-H2* GGCAAATAGGAAATATCATTC. The nuclear RAG1 gene was amplified using the primers Chon-Rag1-S024a CAGATCTTCCAGCCTTTGCATC and Chon-Rag1-R022a CTGAAACCCCTTTCACTCTATC (Iglésias et al. 2005). The nuclear ITS2 subunit and flanking 5.8S and 28S short sequences were PCR amplified using the primers FISH5.8SF TTAGCGGTGGATCACTCGGCTCGT and FISH28SR TCCTCCGCTTAGTAATATGCTTAAATTCAGC (Pank et al. 2001). All PCRs were performed in a total volume of 25 µL consisting of 1× reaction buffer, 2.7 mM $MgCl_2$ for cyt *b* and RAG1, 3 mM $MgCl_2$ for ITS-2, 200 µM dNTPs, 0.4 µM of each primer and 0.5 units of GenScript Taq polymerase (GenScript, USA). The thermocycler profile for the PCRs consisted of initial denaturation at 95 °C for 2 min, then 30 cycles of 95 °C for 30 s, 57 °C for 30 s and 72 °C for 1 min, followed by a final extension at 72 °C for 10 min and a 4 °C soak. PCR amplicons were then sequenced in both directions using the above primers at the McGill University and Génome Québec Innovation Centre.

Sequence data generated in this study are available on GenBank (KP059833-KP059876). All mtDNA sequences were aligned with those from Murray et al. (2008) obtained from GenBank (EF090943–EF090963) using SEQUENCHER 5.0 (GeneCodes, Ann Arbor, MI), trimmed to 702 bp, and a statistical parsimony (95 %) haplotype network was constructed using TCS 1.21 (Clement et al. 2000). Sequences obtained for both nuclear markers were aligned with sequences from Pacific sleeper shark specimens that were provided by the National Marine Fisheries Service, Alaska. Species-specific SNP polymorphisms were identified for both RAG1 (position 607; C: *S pacificus*, T: *S. microcephalus*) and ITS2 (position 635; C: *S. pacificus*, A: *S. microcephalus*).

Gillnet fishery and Greenland shark bycatch

All Canadian directed Greenland halibut commercial fishing operations in Baffin Bay (NAFO Div. 0A) are required to have one hundred percent onboard observer coverage (DFO 2014). Although, several observer companies are employed in the region, a Newfoundland and Labrador (NFL)-based observer company (Seawatch Inc.) is the only one that reports count and weight (kg) of Greenland shark bycatch. Data from 2008 to 2011 were requested from Fisheries and Oceans Canada, NFL Region; all data came from the Greenland halibut gillnet fishery concentrated on the southeast shelf slopes of Baffin Basin (Fig. 3). In total, 1,647 hauls from 26 trips were observed during the 4-year sampling period, representing 77.5 % of the total gillnet fishing effort (total number of hauls) that operated in Baffin Bay during that time. Fishing occurs during the ice-free season, from July to November with peak effort from August to October. For specific details on the operation of this fishery, see Cosandey-Godin et al. (2014). Greenland halibut is also fished by trawlers; however, no count information on bycatch was available.

For each haul, data on the number of Greenland shark bycatch and total weight (kg - estimated by onboard

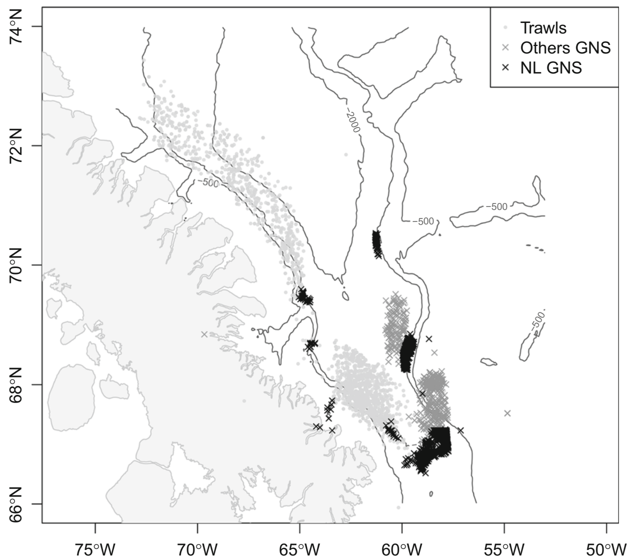

Fig. 3 Map of Baffin Bay showing the spatial distribution of total Greenland halibut (*Reinhardtius hippoglossoides*) fishing effort by trawl and gillnet between 2008 and 2011; GNS = gillnets, NL GNS = observer gillnet data used in this study where weight and count data for Greenland sharks (*Somniosus microcephalus*) were available

observers), the location of the net (start of the haul) and the depth of the gear were available. As a result, individual shark weight was only available when one shark was captured per haul. For these sharks, total length was estimated using the known length–mass relationship, $\ln M = -12.2 + 3.13 \ln TL$ for Greenland sharks (MacNeil et al. 2012). Results were aggregated per month and locations mapped to show the seasonal and spatial distribution of Greenland shark bycatch. Data analyses and mapping were performed using R version 3.1.0 (R Core Team 2013).

Given limited data on stage of sexual maturation with size are available for Greenland sharks (Yano et al. 2007), we adopted the following categorization for animals included in this study: (1) juvenile animals were classified ≤200 cm TL, (2) subadults male and females 200–300 cm TL and 200–450 cm TL, respectively, and mature male and female >300 cm TL and >450 cm TL, respectively. The juvenile-subadult size division was based on the first increase in uterus and testes mass in females and males (Yano et al. 2007). For the Greenland halibut gillnet fishery bycatch data, sex of individual sharks was not available; consequently, subadult and mature sharks were grouped as 200–450 and >450 cm TL, respectively.

Results

Over the three-year scientific survey, a total of 54 Greenland sharks ranging in size from ~100 to 312 cm TL were caught on longlines in Scott Inlet/Sam Ford Trough ($n = 52$) and during bottom trawl surveys at the entrances to Scott Inlet/Sam Ford Trough ($n = 2$; Table 1; Fig. 2). Of these sharks, 22 individuals (42.3 %) were categorized as juveniles of ≤200 cm TL (Table 1; Fig. 2). In 2011, a total of eight Greenland sharks were caught, of which juveniles included two females of ~100 and 175 cm TL and two unknown sex of ~125 and 200 cm TL (Table 1). During the 2012 survey, a total of 17 Greenland sharks were caught of which five were ≤200 cm TL, including the smallest captured male of 117 cm TL (Table 1; Fig. 4a) and a male of 165 cm TL. One female shark of 192 cm TL was cannibalized while hooked, a second female of 170 cm TL appeared in poor condition from past wounds to the gill region and a third shark of 200 cm escaped from the line (Table 1). During the 2013 survey, a total of 27 sharks were caught in Scott Inlet/Sam Ford Trough and two were caught at the entrances, including 13 animals ≤200 cm TL. Of the five smallest sharks caught, one measured ~100 cm TL (escaped from line; unknown sex), a male of 146 cm TL (Fig. 4b), a female of 150 cm TL (Fig. 4c), a female of 157 cm TL and a male of 165 cm TL (Table 1). Over the three-year period, there were no recaptures of animals previously caught and marked with external dart tags.

For 44 individual sharks caught in 2012 and 2013, 702 bp of the mtDNA cyt *b* gene was recovered. A total of 11 cyt *b* haplotypes were found among the samples: seven previously undescribed Greenland shark haplotypes, three known Greenland shark haplotypes (H16, H18, H20; see Murray et al. 2008) and one known Pacific sleeper shark haplotype (H4; Table 1; Fig. 5). Among the *S. microcephalus* mtDNA haplotypes, twelve variable sites were found among the *S. microcephalus* samples, with a haplotype diversity (H_d) of 0.692 and nucleotide diversity (Pi) of 0.00207. The two individuals with Pacific sleeper shark mtDNA signatures, including a 150 cm TL individual, carried the *S. pacificus* H4 haplotype (described by Murray et al. 2008; Table 1). No size-specific genetic partitioning was observed among juvenile/subadult and mature Greenland sharks (Fig. 5). All 44 sharks possessed the species-specific SNPs for *S. microcephalus* at the RAG1 and ITS2 markers.

Of the 1,647 hauls observed in the Greenland halibut gillnet fishery between 2008 and 2011, 147 recorded Greenland shark bycatch. Of these, 65 hauls reported one shark and one estimated individual weight (kg), ranging from 5 to 500 kg with a mean of 107.4 kg per shark. The smallest shark was estimated at ~82.4 cm TL while the largest was approximately ~359 cm TL (Fig. 6). A total of 38 sharks were categorized as juveniles with a TL of ≤200 cm. These sharks were observed from July–October to the south and north of a fishery closure area (Fig. 6). The median TL estimates of bycatch Greenland sharks

Table 1 Greenland sharks (*Somniosus microcephalus*) captured in and at the entrances to Scott Inlet/Sam Ford Trough in 2011, 2012 and 2013

Capture date	Fishing gear[a]	Location[b]	Size (TL—cm)	Sex[d]	Genetics[e]
2011					
07/09/2011	*LG-L*	*SI-IF1*	*100*[c]	*U*	
07/09/2011	*LG-L*	*SI-IF1*	*125*[c]	*U*	
07/09/2011	*LG-L*	*SI-IF1*	*175*[c]	*F*	
07/09/2011	*LG-L*	*SI-IF1*	*200*[c]	*F*	
07/09/2011	**LG-L**	**SI-IF1**	**250**[c]	**F**	
07/09/2011	**LG-L**	**SI-IF1**	**250**[c]	**F**	
07/09/2011	**LG-L**	**SI-IF1**	**250**[c]	**F**	
07/09/2011	**LG-L**	**SI-IF1**	**300**[c]	**F**	
2012					
25/09/2012	*LG-L*	*SI-IF1*	*117*	*M*	*H18*
25/09/2012	*LG-L*	*SI-IF1*	*165*	*M*	*SI-11*
26/09/2012	*LG-L*	*SI-IF1*	*170*	*F*	*H18*
25/09/2012	*LG-L*	*SI-IF1*	*192*	*F*	*SI-20*
25/09/2012	*LG-L*	*SI-IF1*	*200*	*U*	*H18*
26/09/2012	**LG-L**	**SI-IF1**	**214**	**M**	**H18**
25/09/2012	**LG-L**	**SI-IF1**	**220**	**M**	**H18**
25/09/2012	**LG-L**	**SI-IF1**	**245**	**F**	**H18**
26/09/2012	**LG-L**	**SI-IF1**	**250**	**M**	**H18**
26/09/2012	**LG-L**	**SI-IF1**	**254**	**M**	**H18**
25/09/2012	**LG-L**	**SI-IF1**	**256**	**M**	**SI-11**
26/09/2012	**LG-L**	**SI-IF1**	**262**	**F**	**H16**
26/09/2012	**LG-L**	**SI-IF1**	**262**	**M**	**H18**
25/09/2012	**LG-L**	**SI-IF1**	**272**	**F**	**H16**
26/09/2012	**LG-L**	**SI-IF1**	**274**	**M**	**H18**
26/09/2012	**LG-L**	**SI-IF1**	**280**	**M**	**H18**
26/09/2012	**LG-L**	**SI-IF1**	**308**	**F**	**H18**
2013					
24/09/2013	*LG-L*	*SI-IF2*	*100*[c]	*U*	
29/09/2013	*BT*	*SI-E2*	*146*	*M*	*SI-24*
24/09/2013	*LG-L*	*SI-IF2*	*150*	*F*	*H4*
24/09/2013	*LG-L*	*SI-IF2*	*157*	*F*	*SI-22*
19/09/2013	*LG-L*	*SI-IF1*	*165*	*M*	*H18*
24/09/2013	*LG-L*	*SI-IF2*	*172*	*M*	*H20*
18/09/2013	*LG-L*	*SI-IF1*	*176*	*M*	*H16*
19/09/2013	*LG-L*	*SI-IF1*	*180*	*U*	
19/09/2013	*LG-L*	*SI-IF1*	*181*	*M*	*H18*
28/09/2013	*LG-L*	*STF-IF1*	*181*	*M*	*SI-23*
28/09/2013	*LG-L*	*STF-IF1*	*186*	*F*	*SI-23*
28/09/2013	*LG-L*	*STF-IF1*	*189*	*F*	*H18*
18/09/2013	*LG-L*	*SI-IF1*	*194*	*F*	*H18*
18/09/2013	**LG-L**	**SI-IF1**	**216**	**M**	**H18**
24/09/2013	**LG-L**	**SI-IF2**	**250**	**F**	**H4**
29/09/2013	**LG-L**	**STF-IF2**	**257**	**M**	**H20**
19/09/2013	**LG-L**	**SI-IF1**	**257**	**M**	**H18**
24/09/2013	**LG-L**	**SI-IF2**	**267**	**F**	**H16**
29/09/2013	**LG-L**	**STF-IF2**	**275**	**F**	**H18**
19/09/2013	**LG-L**	**SI-IF1**	**280**	**M**	**H18**

Table 1 continued

Capture date	Fishing gear[a]	Location[b]	Size (TL—cm)	Sex[d]	Genetics[e]
19/09/2013	**LG-L**	**SI-IF1**	**281**	**M**	**H18**
18/09/2013	**LG-L**	**SI-IF1**	**285**	**F**	**H18**
27/09/2013	**BT**	**SI-E1**	**285**	**M**	**H18**
18/09/2013	**LG-L**	**SI-IF1**	**289**	**F**	**H20**
18/09/2013	**LG-L**	**SI-IF1**	**295**	**M**	**H18**
19/09/2013	**LG-L**	**SI-IF1**	**305**	**M**	**SI-20**
19/09/2013	**LG-L**	**SI-IF1**	**307**	**F**	**H16**
19/09/2013	**LG-L**	**SI-IF1**	**311**	**F**	**SI-27**
24/09/2013	**LG-L**	**SI-IF2**	**312**	**F**	**H20**

Juveniles ≤200 cm TL are highlighted in italic; subadult and mature adult sharks >200 cm TL in bold

[a] *LG-L* longline, *BT* bottom trawl

[b] For locations of longline sets and bottom trawls, see Fig. 2. Location codes are a combination of fjord name and sub-fjord site. *SI* Scott Inlet, *SFT* Sam Ford Trough, *IF* in fjord, *E* entrance to fjord

[c] Total length (TL—cm) of shark estimated by scientific crew on board research vessel using landmarks on the side of the ship

[d] *M* male, *F* female, *U* unknown

[e] Haplotype; see Fig. 5

increased over the fishing season, suggesting smaller sharks are more prevalent in the earlier months of fishing (July–September), whereas larger individuals are more abundant later in the season (October–November; Fig. 6). Median depth of trawl capture was similar for all size sharks at ~1,000 m (Fig. 7).

Discussion

These data represent the first documentation of repeated captures of juvenile Greenland sharks over three years at one location in the Eastern Canadian Arctic (Scott Inlet/Sam Ford Trough) and summarize their occurrence as bycatch in gillnet fisheries at two sites in offshore waters of Baffin Bay. The capture of juvenile sharks in both fjords and offshore waters may indicate either varied birthing strategies within the Greenland shark population with juveniles having defined home ranges in inshore and offshore waters or the occurrence of complex large-scale movements during this early life stage. More detailed data on fine-scale movements and habitat use of these juvenile animals are required to resolve this. These data also document the first record of *S. pacificus* mtDNA genetic signatures outside of the Pacific Ocean.

There are several plausible explanations for the occurrence of juvenile Greenland sharks in both inshore and offshore waters. Juveniles of most coastal shark species remain resident in nursery grounds with restricted home ranges for periods of time ranging from months (Duncan and Holland 2006) to years (Morrissey and Gruber 1993a), following which individual home ranges expand (Morrissey and Gruber 1993b; Heupel et al. 2007). Given the capture of Greenland sharks approximating the range of reported birth sizes (~40–100 cm TL) in Scott Inlet/Sam Ford Trough and the description of two 100 cm sharks that were suspected to be 10–15 days old in coastal waters near Jan Mayen Island, Norway (Kondyurin and Myagkov 1983), it is plausible that Greenland sharks are birthed in coastal regions. It is possible, however, that the two 100-cm sharks identified by Kondyurin and Myagkov (1983) were in fact basking sharks (*Cetorhinus maximus*). These sharks were reported to have yolk remains, while the most detailed examination of a near-term Greenland shark fetus found no evidence of this (Koefoed 1957). If this were the case, the occurrence of larger juvenile sharks in both inshore and offshore waters would indicate these animals undertake large-scale movements at this life stage, similar to those previously reported for juvenile dusky (*Carcharhinus obscurus*) and scalloped hammerhead sharks (*Sphyrna lewini*) (Klimley 1987; Hussey et al. 2009).

Alternatively, the occurrence of juvenile Greenland sharks in both protected inshore and exposed offshore waters could indicate that Greenland sharks exhibit two distinct birthing and/or nursery strategies. This disparity in birthing location is not typically considered for sharks in one geographic region, but both sheltered coastal lagoonal nurseries and exposed continental shelf nurseries have been observed for scalloped hammerhead sharks in Hawaii and South Africa, respectively (Fennessy 1994; Duncan and Holland 2006). Similarly, juvenile lemon sharks (*Negaprion brevirostris*) reside in sheltered lagoonal nurseries in Bimini, Bahamas (Feldheim et al. 2002), while young sharks at Cape Canaveral, Florida, occupy the shallow

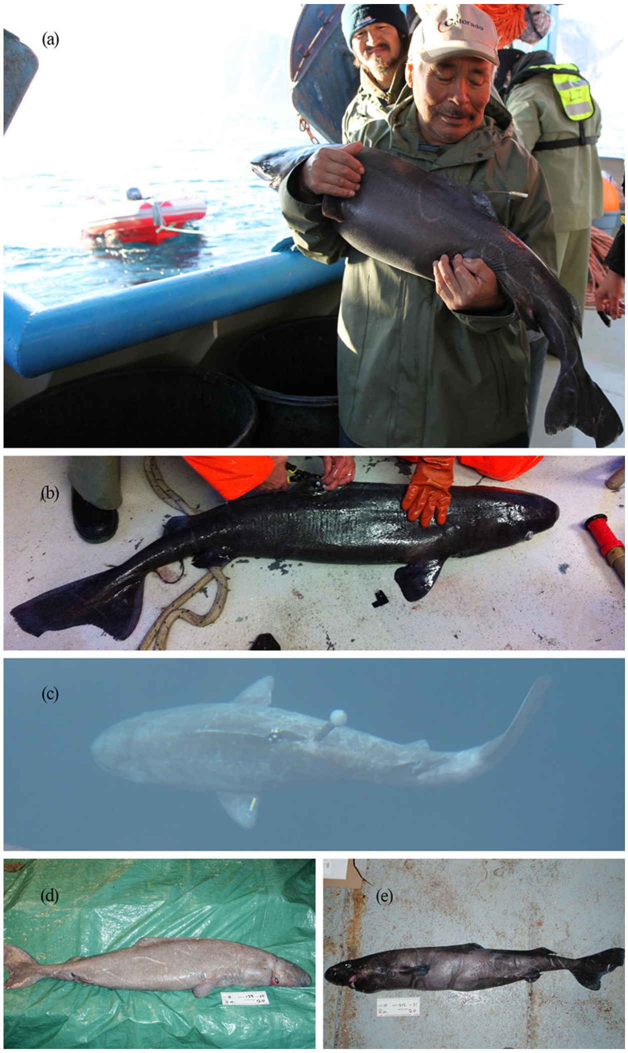

Fig. 4 Photographic documentation of captured juvenile Greenland sharks (*Somniosus microcephalus*); **a** smallest accurately measured juvenile Greenland shark captured in Scott Inlet, a male of 117 cm TL; **b** a 146 cm TL male captured in a biodiversity survey bottom trawl; **c** a 150 cm TL female shark swimming away following release (note this individual has a pop-up archival satellite tag attached to the dorsal fin); **d**, **e** small sharks caught in the Greenland halibut gillnet fishery in 2011; scale bar is equal to 15 cm. (Image from Department of Fisheries and Oceans Canada). Note high variation in *color* between individuals previously described in larger Sleeper sharks (see review by MacNeil et al. 2012). (Color figure online)

waters of exposed beaches and undertake seasonal movements of several hundred kilometers (Reyier et al. 2008, 2014). This demonstrates that birthing and nursery locations can be variable within a single species. Nevertheless, the repeated occurrence of juvenile sharks in Scott Inlet/Sam Ford Trough over a 3-year period, at two specific sites in offshore waters and their rare occurrence in other Canadian Arctic regions, fulfills two of the nursery ground criteria defined by Heupel et al. (2007): (1) the area is used repeatedly across years and (2) juvenile sharks are more commonly observed in the area compared to other areas.

The capture of juvenile Greenland sharks ≤200 cm TL in Cumberland Sound and Lancaster Sound during scientific fishing is rare, and only two small individuals ≤150 cm have previously been recorded in the Canadian Arctic (Fisk et al. 2002; both 135 cm TL—caught in Davis Strait but exact location unknown). This observation is further confirmed by the capture of only subadult and mature sharks >200 cm TL across the entire Canadian Arctic. Indeed, Beck and Mansfield (1969) reported the capture of Greenland sharks >200 cm in gill nets set in Koluktoo Bay and Pond Inlet, and Skomal and Benz (2004) reported sharks ranging from 190 to 355 cm fork length (FL) around Victor Bay (Fig. 1). Moreover, recent studies that conducted pop-up archival satellite tagging of sharks in Cumberland Sound, off Nova Scotia and Svalbard reported only catching larger sharks ranging in size from 243 to 516 cm TL (Fisk et al. 2012; Campana et al. 2014). These data indicate that Greenland sharks of >200 cm TL occur across a broad geographic area, which is in agreement with the bycatch data from Greenland halibut gillnet fisheries. This suggests that smaller Greenland sharks may occur over more restricted ranges and consequently Scott Inlet/Sam Ford Trough and the two offshore sites may represent core juvenile habitats within our sampling area in the Canadian Arctic. The occurrence of small Greenland sharks in other regions of the Arctic is also rare. Nielsen et al. (2014) reported the capture of only four sharks ≤200 cm around Greenland from scientific surveys and commercial fisheries catches since 1998, with these all occurring in a relatively defined region on the west coast (Fig. 1). Rusyaev and Orlov (2013) reported 23 sharks ≤200 cm TL (30.7 % of total) with 13 individuals <150 cm TL. Most of these sharks were caught in the southeastern Barents Sea within the same latitudinal range as the juveniles caught in Scott Inlet/Sam Ford Trough and observed as bycatch in the gillnet fishery (Rusyaev and Orlov 2013; Fig. 1). In addition, these juvenile sharks were caught offshore.

At-sea observer data are the best available fishery-dependent information to monitor bycatch species, but we caution that these data are influenced by many variables such as effort, fishing location and differences in observer practices, among other factors. When considering this and taking into account that the largest catch (by mass-kg) of Greenland sharks in Baffin Bay is associated with Greenland halibut trawling activities rather than gillnet (Davis et al. 2013), it is certainly possible that juvenile Greenland sharks may occur at other Arctic locations outside of our study sites, including both coastal and offshore sites. Furthermore, our TL estimates from bycatch data were derived from estimated individual total weight as opposed to in situ measurements. Nonetheless, the present study reports the best available information on the seasonal and size

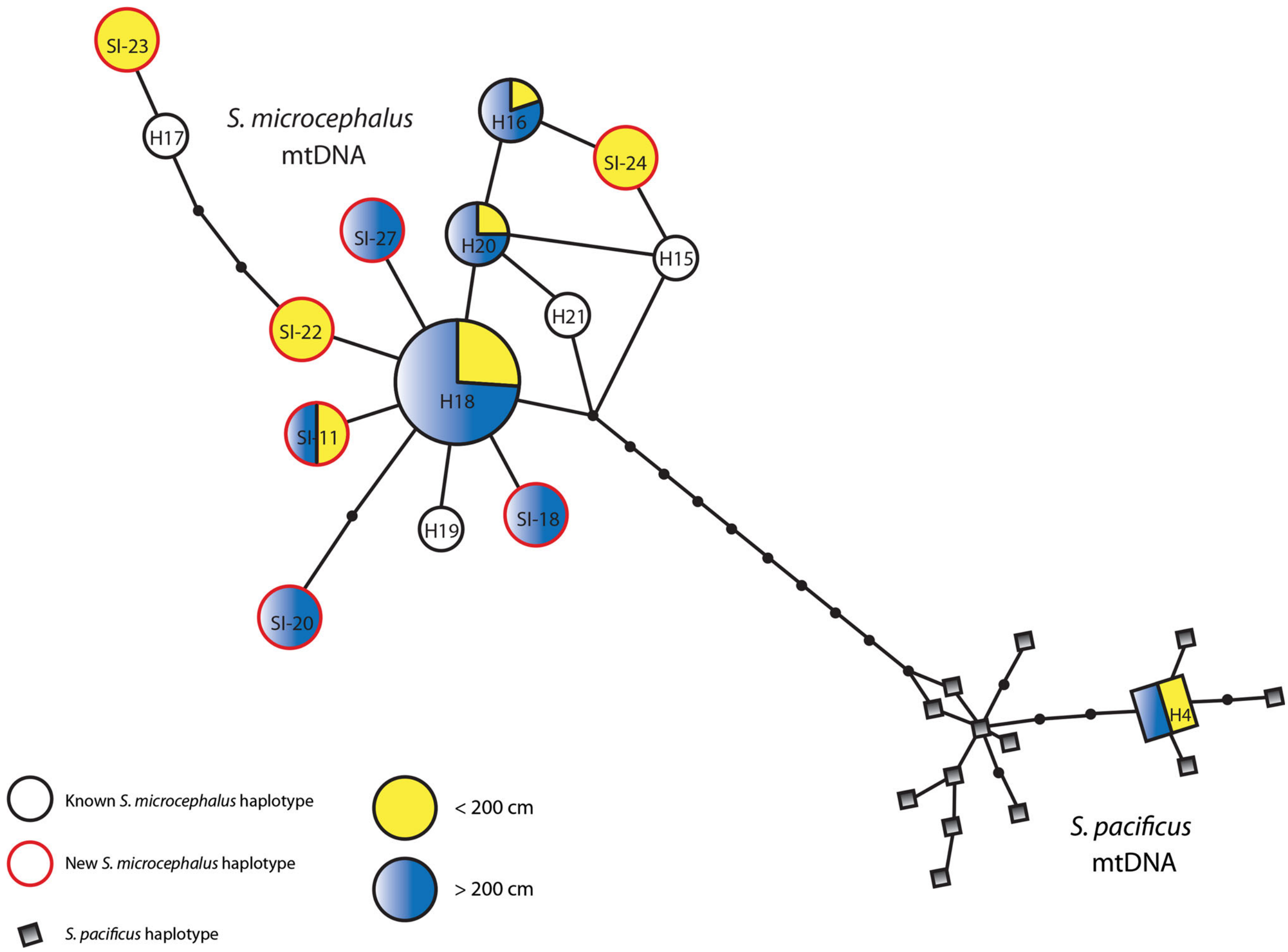

Fig. 5 Statistical parsimony haplotype network of sleeper sharks (*Somniosus*) sampled from Scott Inlet/Sam Ford Trough, with known Greenland (*Somniosus microcephalus*) and Pacific sleeper (*Somniosus pacificus*) shark haplotypes reported from the literature, using 702 bp of the mtDNA cytochrome *b* gene (cyt *b*). *Black circle* outline indicates known and *red circle* (*dark gray*) outline indicates newly reported Greenland shark haplotypes; *yellow* (*light gray*) and *blue* (*medium gray*) coloring in *circles* represent the proportions of detected haplotypes in juveniles (≤200 cm TL) and subadults/adults (>200 cm TL), respectively. *White circles* indicate known Greenland shark haplotypes that were not sampled, *solid black circles* represent missing haplotypes and *squares* indicate known Pacific sleeper shark haplotypes. (Color figure online)

distribution of Greenland shark bycatch in the offshore region of Baffin Bay and demonstrates that juvenile sharks (≤200 cm) are present.

Genetic analysis identified all but two individual sharks sampled in Scott Inlet/Sam Ford Trough as Greenland sharks at all three molecular markers. The two admixed individuals showed Greenland shark nuclear signatures but a Pacific sleeper shark haplotype (H4) following Murray et al. (2008). Genetic samples were not available for the juvenile Greenland sharks reported as bycatch in the Greenland halibut gillnet fisheries in Baffin Bay, but discussions with Fisheries and Oceans Canada managers and fishery observers, and further photographic evidence (Fig. 3d, e and see Fig. 1d in Davis et al. 2013), indicate correct species identification. Surprisingly, a greater amount of mtDNA genetic diversity than expected was detected among Greenland sharks sampled from Scott Inlet/Sam Ford Trough. Of the seven known *S. microcephalus* cyt *b* haplotypes, three were sampled at our site, and an additional seven previously undescribed haplotypes were recovered. Of particular interest is the occurrence of *S. pacificus* mtDNA haplotypes in individuals carrying nuclear *S. microcephalus* signatures, suggesting a more complex evolutionary history among Arctic sleeper sharks than was previously thought. In lieu of shared ancestry, their nearly identical morphologies, diet and life histories, these genetic data are consistent with the possibility of hybridization among Greenland and Pacific sleeper sharks. Additional data are needed, however, to assess the scale of interspecific gene flow.

In both Scott Inlet/Sam Ford Trough and offshore Baffin Bay, juvenile Greenland sharks were caught in deep waters

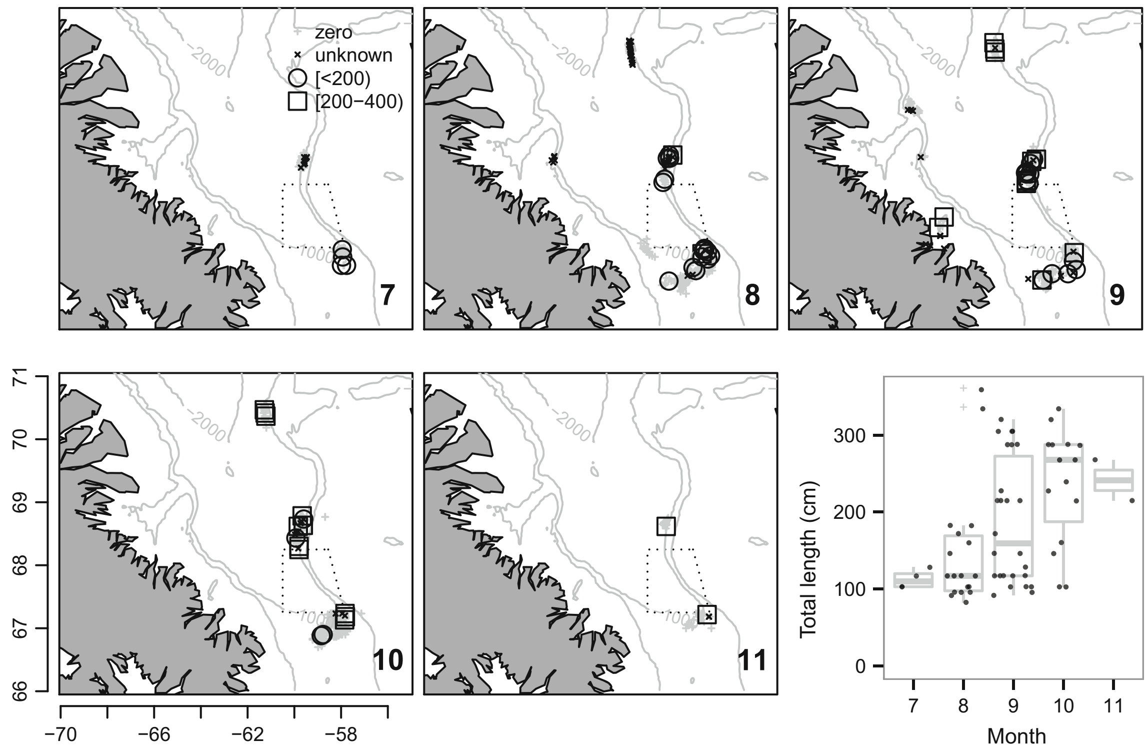

Fig. 6 Seasonal distribution by month (July–November) of juvenile (≤200 cm TL; *open circles*) and subadult/adult (>200 cm TL; *open squares*) Greenland sharks (*Somniosus microcephalus*) captured by the Greenland halibut (*Reinhardtius hippoglossoides*) gillnet fishery. 'Zero' shows the distribution of hauls where no Greenland shark bycatch was reported and 'unknown' the distribution of hauls where >1 Greenland shark was captured and consequently total length of individual animals could not be estimated. The *dashed box* demarcates the fishing closure area for the protection of narwhal and deep sea corals (DFO 2007). The *boxplot* (*bottom right*) shows the occurrence of individual animals by size (TL, cm) and month

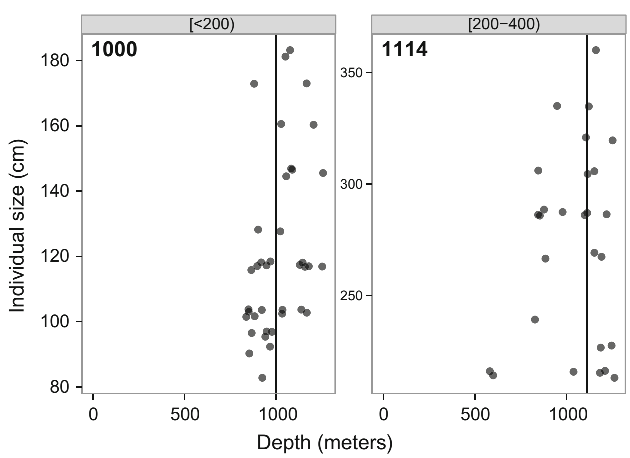

Fig. 7 Depth of capture of juvenile (≤200 cm TL) and subadult/adult (>200 cm TL) Greenland shark (*Somniosus microcephalus*) bycatch in the Greenland halibut (*Reinhardtius hippoglossoides*) gillnet fishery in Baffin Bay where observer mass and count data allowed estimation of animal length

(~1,000 m). Similarly, Yano et al. (2007) and Nielsen et al. (2014) noted that small sharks recorded off Greenland were caught in deep water >900 m. Larger sharks, however, were present in both systems and were caught at the same time, indicating that both the deep water fjords and offshore habitats are used by sharks of various sizes. Size-based segregation between juvenile and subadult/adult Greenland sharks by habitat or depth therefore does not appear to occur.

Identifying juvenile Greenland shark habitat in the Canadian Arctic provides a first step to understanding this poorly known life stage. This is pertinent given increasing commercial fishing in the region (Christiansen et al. 2014), the current development of coastal artisanal fisheries to improve the economic and social status of Inuit communities (Dennard et al. 2010; Zeller et al. 2011) and the overlap in distribution between Greenland sharks and commercially important Greenland halibut (Peklova et al. 2012). Determining residency, movement patterns and home ranges with increasing animal size, resolving species identification and population structure and improving observer data collection in commercial fisheries through recording actual size of animals will further our understanding of the habitat preferences and spatial dynamics of Greenland sharks in this extreme environment. The current and ongoing consideration of Scott Inlet/Sam Ford Trough as a marine protected area (Parks Canada National Marine

Conservation Area) and the occurrence of juvenile Greenland sharks surrounding the fishery closure area for narwhal and deep sea corals (DFO 2007) provide an important step for protecting identified juvenile Greenland shark habitat in the Canadian Arctic.

Acknowledgments This research was supported by Government of Nunavut funding to N.E.H., K.J.H. and A.T.F. and Ocean Tracking Network and Canada Research Chair funding to A.T.F. A.G. was supported by an NSERC Industrial Postgraduate Scholarship and funding from WWF-Canada. We thank the crew of the Nuliajuk and the Government of Nunavut for logistical support in the field to undertake fishing. S.M. Rusyaev is thanked for providing the capture locations of small Greenland sharks in the Barents Sea.

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