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Impacts of food web structure and feeding behavior on mercury exposure in Greenland Sharks (*Somniosus microcephalus*)

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HIGHLIGHTS

- THg significantly increased with $\delta^{15}N$ from invertebrates to Greenland Sharks.
- THg increased with $\delta^{15}N$ at a faster rate through the pelagic than benthic food web.
- Benthic primary consumers had higher THg than pelagic counterparts.
- Benthic and pelagic Greenland Shark prey did not consistently differ in THg.
- THg among individual sharks was not explained by size, gender or feeding behavior.

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ABSTRACT

Benthic and pelagic food web components in Cumberland Sound, Canada were explored as sources of total mercury (THg) to Greenland Sharks (*Somniosus microcephalus*) via both bottom-up food web transfer and top-down shark feeding behavior. Log_{10}THg increased significantly with $\delta^{15}N$ and trophic position from invertebrates (0.01 ± 0.01 $\mu g \cdot g^{-1}$ [113 ± 1 $ng \cdot g^{-1}$] dw in copepods) to Greenland Sharks (3.54 ± 1.02 $\mu g \cdot g^{-1}$). The slope of the log_{10}THg vs. $\delta^{15}N$ linear regression was higher for pelagic compared to benthic food web components (excluding Greenland Sharks, which could not be assigned to either food web), which resulted from THg concentrations being higher at the base of the benthic food web (i.e., in benthic than pelagic primary consumers). However, feeding habitat is unlikely to consistently influence shark THg exposure in Cumberland Sound because THg concentrations did not consistently differ between benthic and pelagic shark prey. Further, size, gender and feeding behavior (inferred from stable isotopes and fatty acids) were unable to significantly explain THg variability among individual Greenland Sharks. Possible reasons for this result include: 1) individual sharks feeding as generalists, 2) high overlap in THg among shark prey, and 3) differences in turnover time between ecological tracers and THg. This first assessment of Greenland Shark THg within an Arctic food web revealed high concentrations consistent with biomagnification, but low ability to explain intra-specific THg variability. Our findings of high THg levels and consumption of multiple prey types, however, suggest that Greenland Sharks acquire THg through a variety of trophic pathways and are a significant contributor to the total biotic THg pool in northern seas.

1. Introduction

Warming surface air temperatures and concomitant declines in ice-cover will continue to alter the emissions, transport and bioavailability of contaminants in the Arctic (AMAP, 2011). Climate-mediated shifts in food web structure may also influence body burdens of primarily dietary-derived contaminants (e.g., mercury, hereafter Hg) in Arctic food webs. Because Hg biomagnifies and can reach levels that are harmful to Arctic species (Tartu et al., 2013), identifying the major Hg sources and trophic pathways by which Hg is transferred to Arctic predators is a priority.

Food web characteristics, including concentrations of Hg at the base of food webs ('basal' Hg; e.g., levels that are acquired by primary producers via the surrounding water) and food chain length, partially dictate the amount of Hg ultimately transferred to top predators (AMAP, 2011; Lavoie et al., 2010; St. Louis et al., 2011). Within-species differences in predator feeding behavior are also important, and individuals that feed either on higher trophic position prey (St. Louis

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et al., 2011) or in more contaminated habitats (Loseto et al., 2008a), often for reasons associated with size (Loseto et al., 2008b) or gender (Cardona-Marek et al., 2009), can acquire higher Hg concentrations compared to other individuals within a population. Exploring both the structure of the food web and the feeding behavior of the organism in question (e.g., by combining stable isotopes and fatty acids as dietary tracers) has successfully explained intra-specific Hg burdens in Arctic marine mammals (e.g., beluga whales: Loseto et al., 2008a, 2008b; polar bears: Cardona-Marek et al., 2009; St. Louis et al., 2011). Much less is known, however, about the Hg levels of, and Hg trophic transfer pathways to, predatory marine fish in the Arctic.

The Greenland Shark (*Somniosus microcephalus*) is one of the only two sharks known to regularly inhabit seasonally ice-covered seas in the Northern hemisphere (the other being the Pacific Sleeper Shark, *Somniosus pacificus*). Greenland Sharks are large, potentially long-lived and abundant (MacNeil et al., 2012) predators and scavengers of benthic and pelagic fishes and marine mammals (Fisk et al., 2002; Leclerc et al., 2012). Greenland Sharks from temperate seas can accumulate high muscle Hg levels (McMeans et al., 2010) and one previous study reported that liver Hg concentrations were higher in Greenland Sharks than in Pacific Sleeper Sharks (McMeans et al., 2007). However, no study to date has reported Hg levels of Greenland Sharks within an Arctic food web.

The goal of the present study was to explore if and how food web structure and feeding behavior explain total Hg (THg) levels of Greenland Sharks sampled in a seasonally ice-covered ecosystem (Cumberland Sound, Baffin Island, Nunavut, Canada). Food web characteristics (i.e., basal Hg levels and biomagnification) were explored considering: 1) the entire food web and, 2) benthic- and pelagic-based food web components separately (to explore a possible habitat effect on Hg bioavailability and transfer rates). The potential influence of feeding behavior on Greenland Shark THg levels was then assessed by determining whether shark size, gender, $\delta^{15}N$, $\delta^{13}C$ or fatty acids (applied as dietary tracers) explained a significant amount of THg variability among individuals. The data presented here will help generate a more complete picture of Hg transfer through Arctic food webs by providing data for a large and abundant, but poorly studied, carnivore, and may be useful for understanding the possible consequences of climate-driven food web structure shifts on Greenland Shark Hg levels.

2. Methods

2.1. Species sampling

Sampling took place during August 2007–2009 and April 2008–2009 within the area encompassed by Pangnirtung fjord and up to 30 km northwest and 30 km southwest from the mouth of the fjord into Cumberland Sound (see the KML file associated with this article for a map of sampling locations). The sampling area receives freshwater inputs from River Duval, melting permafrost and upland glaciers, although the quantity of these inputs has not, to our knowledge, been quantified.

Benthic invertebrates were sampled via benthic bottom traps or Ponar grabs and pelagic invertebrates via a plankton net (243 μm mesh). Greenland Sharks and benthic fishes were captured via bottom long lines, except for Shorthorn Sculpin (*Myoxocephalus scorpius*, captured using baited fishing line). Pelagic fishes were sampled via dip nets (Capelin, *Mallotus villosus*) or gill nets (Arctic Char, *Salvelinus alpinus*) and seals were collected during Inuit subsistence hunts. Fork and total lengths were collected for individual sharks and fishes, respectively, and standard length (snout to tail) was recorded for seals. Greenland Shark stomach contents were identified to as low a taxonomic resolution as possible, typically to the genus or species level.

Grazing amphipods (*Gammarus oceanicus*), scavenging amphipods (*Onisimus* spp.), shrimp (unidentified sp.), polychaetes (unidentified sp.), copepods (*Calanus hyperboreus*) and *Themisto* (*Themisto libellula*, a carnivorous amphipod) were sampled whole, and multiple individuals (5–20) were pooled in to obtain sufficient material for THg and stable isotope ($\delta^{15}N$, $\delta^{13}C$) analysis. Mantle was sampled from individual clams (*Hiatella arctica*) and foot was sampled from individual limpets (*Tectura testudinalis*) and whelks (*Buccinum cyaneum*) for both THg and stable isotope analyses. Muscle was sampled from all fishes and seals for THg and stable isotopes. Fish muscle was also sampled for fatty acid analysis, but blubber was sampled for this purpose from seals. A single sample was used for both THg and stable isotope analyses and a separate sample was taken (from each individual fish and seal) for fatty acids. All samples were frozen at −20 °C (THg and stable isotope samples) or −80 °C (fatty acid samples) in cryovials within 1 h from the time of collection and kept frozen until analysis.

2.2. Stable isotope and fatty acid analysis

Stable isotopes were analyzed as previously described (McMeans et al., 2013b). Briefly, sub-samples were taken, freeze-dried (48 h) and homogenized for stable isotope analysis, leaving the remaining wet (frozen) tissue for THg analysis. Lipids were removed (2:1 chloroform:methanol) prior to weighing (into tin capsules) and running on a continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Electron) for determination of $\delta^{15}N$ and $\delta^{13}C$ values. Stable isotopes are expressed as ratios (R) of heavy to light nitrogen or carbon in the sample relative to that of a standard as follows: $\delta X = 1000 * [R_{sample} \cdot R_{standard}^{-1}]$ where X = ^{15}N or ^{13}C and R = ^{15}N:^{14}N or ^{13}C:^{12}C. Precision (1SD) based on replicate analysis ($n = 159$) of NIST (National Institute of Standards and Technology) standard, bovine muscle was 0.13‰ for $\delta^{15}N$ and 0.07‰ for $\delta^{13}C$.

Samples were analyzed for fatty acids as previously described (McMeans et al., 2012) by homogenizing freeze-dried (48 h) tissues in 2:1 chloroform:methanol and generating fatty acid methyl esters (via sulfuric acid in methanol, 1:100), which were then separated on a Hewlett Packard 68900 GC and identified using known standards. Individual fatty acids are reported on a proportional basis (i.e., individual fatty acid mass fractions · mass fraction of all measured fatty acids^{-1}, both on a dry weight (dw) basis, and expressed as %).

2.3. Mercury analysis

Total mercury (THg) was determined via atomic absorption spectrophotometry on a DMA-80 Direct Mercury Analyzer (Milestone Inc., Shelton, CT, USA). This system requires no sample pre-processing and accepts both wet and dry samples. We predominantly analyzed wet samples, except for copepod, limpet, polychaetes, clam, shrimp and *Themisto*, which were freeze-dried in their entirety to ensure sufficient material for both stable isotopes and THg. To account for different % moisture contents among our samples, we converted all wet weight (ww) values to dw values using the sample's % moisture (calculated as tissue weight loss of a sub-sample after oven-drying overnight). There was a good agreement between the THg values from samples analyzed both as: 1) dry, and 2) wet, and then converted to dw values using the sample's % moisture content (THg mean ± SD of $n = 12$ Arctic Skate muscle samples: 2.03 ± 1.18 and 2.08 ± 1.18 μg·g^{-1}, dw, respectively). Tissue % moisture was determined following freeze-drying and used to convert dw to ww values (reported for comparison to previous studies, see subsequent section) for samples that were analyzed dry.

Duplicates sample runs ($n = 7$) had coefficients of variation ranging from 1.2 to 15.5%. Two NIST standard reference materials (DOLT-4, DORM-3) were run with each batch of 32 samples. The measured value (mean ± SD, $n = 9$ for each standard) of DOLT-4 was 2.68 ± 0.35 μg·g^{-1} (certified value 2.58 ± 0.22 μg·g^{-1}) and of DORM-3 was 0.35 ± 0.03 μg·g^{-1} (certified value 0.38 ± 0.06 μg·g^{-1}). Approximately

40 mg of dry invertebrate tissue was weighed for THg analysis. Wet sample weights were approximately 200 mg for invertebrates and fish, 150 mg for seal, and ranged from 11 to 90 mg for Greenland Shark. The lower sample weights used for Greenland Sharks (due to higher THg in this tissue) did not impact THg measurements because there was no significant difference (based on Welch's t test, $P > 0.05$) between a subset of $n = 19$ Greenland Shark muscle samples that were analyzed both: 1) via the DMA-80 system as described above ($3.62 \pm 1.23\ \mu g \cdot g^{-1}$, dw), and 2) from larger sample weights (2 g) that were previously analyzed via a Varian SpectrAA-300 Atomic Absorption Spectrometer (Varian Inc, Palo Alto, CA, USA) following microwave digestion ($3.87 \pm 1.18\ \mu g \cdot g^{-1}$, dw). Further, we obtained accurate THg values for DOLT-4 on the DMA-80 (see above) using sample weights of 11 to 25 mg. THg was analyzed in the present study, although MeHg is the predominant biomagnifying form of Hg. However, most of the THg in upper trophic levels is present as MeHg, and THg also biomagnifies through Arctic food webs, although at a lower rate than MeHg (Rigét et al., 2007; Van der Velden et al., 2013).

2.4. Data analyses

We compiled a data set consisting of new and previously published stable isotope and fatty acid data and new THg data. Large portions of the stable isotope data generated from our field operations in Cumberland Sound were previously published to explore summer (August) food web structure (McMeans et al., 2013b), organic contaminant biomagnification (McKinney et al., 2012), and the diet of beluga (Marcoux et al., 2012) and Greenland Halibut (Dennard et al., 2009). Many of the fatty acid data were previously published in McMeans et al. (2013b) and in two separate studies focused on: 1) shark and prey tissue fatty acids (McMeans et al., 2012) and 2) Greenland Shark feeding ecology in Svalbard, Norway as compared to Cumberland Sound (McMeans et al., 2013a). The new stable isotope data (not previously published) included here are for shrimp and *Themisto* (both sampled in April 2008) and, from sampling periods not included in the above studies, for Arctic Skate (April 2009), ringed and harp seals (August 2009) and Greenland Shark (April 2008, 2009). New fatty acid data from April 2009 samples are included here for Shorthorn Sculpin, Greenland Shark, Greenland Halibut and Arctic Skate. The THg data were partially included in a Government of Canada Northern Contaminants Program report (NCP, 2012) but have never been published in a peer-reviewed journal.

Trophic positions ($TP_{consumer}$) were first determined from species $\delta^{15}N$ values via the following equation:

$$TP_{consumer} = TP_{baseline} + \frac{\delta^{15}N_{consumer} - \delta^{15}N_{baseline}}{\Delta^{15}N}. \quad (1)$$

Copepod was used as the baseline ($\delta^{15}N_{baseline} = 9.9‰$, $TP_{baseline}$ assumed to equal 2) and 3.4‰ as the $\Delta^{15}N$ for all species except for seals and Greenland Sharks, for which 2.4 and 2.3‰, respectively, were used as the $\Delta^{15}N$ based on previous recognition that seals (Hobson et al., 1996) and sharks (Hussey et al., 2010) have a lower $\Delta^{15}N$ value. Capelin mean $\delta^{15}N$ (13.6‰) and trophic position (3.1, calculated from Eq. (1)) were used as the baseline for seal and shark trophic position calculations (instead of copepod), so that the lower $\Delta^{15}N$ was only taken into account at the last trophic step (Hussey et al., 2014). Previously published habitat and dietary information (AMAP, 2011; McMeans et al., 2013b) was used to assign species to either the 'benthic' or 'pelagic' food web (Table 1). Values of $\delta^{13}C$ were not used for this purpose because they can overlap among benthic and pelagic species in Cumberland Sound (Dennard et al., 2009; McMeans et al., 2013b).

THg was $\log_{10}$ transformed prior to analysis to improve normality and all THg values were reported as dw unless otherwise stated. For food web structure effects, biomagnification was explored via ordinary least squares (OLS) simple linear regression between $\log_{10}$THg vs. $\delta^{15}N$ and trophic position across the entire food web (i.e., using all samples). Linear regression slopes were also compared between benthic and pelagic food web components using ANCOVA. Greenland Sharks were excluded from the benthic and pelagic food web comparison because individual sharks cannot be exclusively assigned to either food web (e.g., as done previously for beluga, Loseto et al., 2008a). THg was then compared between benthic and pelagic primary consumers (grazing amphipods and limpet vs. copepod, respectively, Table 1), which were used as a proxy for basal THg concentrations. Trophic magnification factors (TMFs), which show

Table 1
Sample size (n), collection month and year, and mean ± SD total mercury (THg) and length (fork length for sharks, total length for fishes, standard length [snout to tail] for seals, not recorded [NA] for invertebrates) of Greenland Sharks and benthic and pelagic food web components from Cumberland Sound. Invertebrate feeding mode is provided in parentheses. (From AMAP (2011) and McMeans et al. (2013b).)

Group	Species	Common name	n	Month	Year	Length (cm)	THg ($\mu g \cdot g^{-1}$) Dry weight	Wet weight
Apex predator	*Somniosus microcephalus*	Greenland Shark	57	August April	2007, 2008 2008, 2009	273.3 ± 31.5	3.54 ± 1.02	1.62 ± 0.52
Benthic								
Invertebrates	*Gammarus oceanicus* (H)	Grazing amphipod	5	August	2008	NA	0.06 ± 0.02	0.01 ± 0.01
	Onisimus spp. (O, S)	Scavenging amphipod	3	April	2008	NA	0.48 ± 0.27	0.19 ± 0.14
	Decapod[1]	Shrimp	4	April	2008	NA	0.11 ± 0.03	0.03 ± 0.01
	Hiatella arctica (O)	Clam	4	August	2008	NA	0.07 ± 0.04	0.02 ± 0.01
	Tectura testudinalis (H)	Limpet	4	August	2008	NA	0.09 ± 0.03	0.02 ± 0.01
	Buccinum cyaneum (C, S)	Whelk	5	August	2008	NA	0.10 ± 0.08	0.02 ± 0.02
	Polychaete[2]	Polychaete	3	August	2008	NA	0.05 ± 0.03	0.01 ± 0.01
Vertebrates	*Amblyraja hyperborea*	Arctic Skate	17	April	2008, 2009	60.1 ± 6.6	2.13 ± 1.04	0.42 ± 0.18
	Reinhardtius hippoglossoides	Greenland Halibut	19	April	2008, 2009	62.0 ± 9.0	0.50 ± 0.24	0.17 ± 0.16
	Myoxocephalus scorpius	Shorthorn Sculpin	7	August	2008	28.7 ± 6.5	0.71 ± 0.37	0.16 ± 0.07
Pelagic								
Invertebrates	*Calanus hyperboreus* (H)	Copepod	5	August	2008	NA	0.01 ± 0.01	0.01 ± 0.00
	Themisto libuella (C)	*Themisto*	4	April	2008	NA	0.09 ± 0.06	0.02 ± 0.01
Vertebrates	*Mallotus villosus*	Capelin	6	August	2008	13.5 ± 1.2	0.06 ± 0.01	0.02 ± 0.01
	Salvelinus alpinus	Arctic char	7	August	2008	56.3 ± 11.9	0.14 ± 0.05	0.04 ± 0.02
	Pusa hispida	Ringed seal	12	August	2008, 2009	107.6 ± 16.5	0.59 ± 0.39	0.38 ± 0.13
	Phoca groenlandica	Harp seal	9	August	2008, 2009	166.4 ± 32.8	1.19 ± 0.24	0.18 ± 0.12

H:herbivore, O:omnivore,C:carnivore,S:scavenger; [1]unidentified shrimp, likely O and S, [2]unidentified polychaete but C based on large jaws.

the increase in THg with each trophic position, averaged across the food web, were calculated using the slope (b) derived from the OLS regression of $\log_{10}$THg vs. trophic position to maintain consistency with previous studies (Fisk et al., 2001; Jardine et al., 2006) as follows:

$$\log_{10}\mathrm{THg} = a + b * \mathrm{TP} \quad (2)$$

$$\mathrm{TMF} = 10^{b}. \quad (3)$$

Regression parameters for the entire food web, as well as for the benthic and pelagic food webs separately, were also estimated with Model II reduced major axis regressions (produces less biased slope estimate when both x and y are measured with error, Quinn and Keough, 2002) and were also obtained from ww THg data for comparison to previous studies.

For feeding behavior effects, ANOVA (followed by Tukey's post hoc comparisons) was first used to compare δ^{15}N, trophic position and THg among Greenland Sharks and dominant prey (based on shark stomach contents, see Results). Due to unequal variances among species, pair-wise Welch's t-tests with non-pooled SD and Bonferroni P adjustments were used for δ^{13}C comparisons. A linear additive model was then run to test for the effects of δ^{15}N (or trophic position which replaced δ^{15}N in a second model), δ^{13}C, length and gender on Greenland Shark THg. Finally, shark THg was regressed (via separate OLS regressions) against: 1) individual fatty acid proportions and 2) principal component scores (PC1, PC2) extracted from a PCA performed on Greenland Shark fatty acids (standardized to a mean of 0 and variance of 1 prior to their inclusion in the PCA). Previous publications provide detailed assessments of Greenland Shark and prey fatty acids (McMeans et al., 2012, 2013a, 2013b). Here, we focused on the following 9 individual fatty acid proportions that successfully discriminate among Greenland Shark prey groups (McMeans et al., 2013a): 1) high in skate and cod: 20:4n−4, 20:5n−3, 22:6n−3, 2) high in Greenland halibut: 20:1n−9, 22:1n−9, 22:1n−11 and 3) high in seal blubber: 16:1n−7, 18:1n−9, 22:5n−3. Fatty acid proportions were logit transformed prior to analysis to meet the assumption of normality (Warton and Hui, 2011).

All response variables and model residuals were investigated for normality (via Shapiro–Wilk tests) and homogeneity of variance (via Levene's tests and plots of residuals vs. fitted values). All analyses were performed in R (R Development Core Team, 2010). The package lmodel2 (Legendre and Legendre, 1998) was used for the Model II regressions and package vegan (Oksanen et al., 2010) for the PCA. Statistical differences discussed from this point forward were significant at the $\alpha = 0.05$ level unless otherwise stated. All values are reported as mean ± 1 SD.

3. Results

3.1. Total mercury biomagnification rates

The Cumberland Sound food web contained 5 trophic levels with Greenland Sharks at the highest trophic position (individual shark δ^{15}N-based estimates ranged from 4 to 5, Fig. 1). Inter-specific THg concentrations ranged from a low of 0.01 ± 0.01 $\mu g \cdot g^{-1}$ (113 ± 1 $ng \cdot g^{-1}$) in copepod to a high of 3.54 ± 1.02 $\mu g \cdot g^{-1}$ in the Greenland Shark (Table 1).

Log_{10}THg significantly increased with both δ^{15}N (Table 2) and trophic position (Fig. 1, "All samples") across the entire food web. Slopes were significantly lower when derived from THg on a dw (Table 2) than a ww basis (Table A1) based on ANCOVA (δ^{15}N: $F_{1,338} = 3.942$, $P < 0.05$; trophic position: $F_{1,338} = 7.201$, $P < 0.01$). Trophic position explained more of the variability in $\log_{10}$THg across the entire food web than did δ^{15}N, based on a higher r^2 (0.738 and 0.657, respectively, Table 2). The TMF for the entire Cumberland Sound food web was 4.9 (Table 2).

Based on ANCOVA, THg increased at a faster rate (i.e., had a significantly higher slope) in the pelagic compared with the benthic food web (Greenland Sharks were excluded from this analysis) as a function of both δ^{15}N ($F_{1,110} = 11.413$, $P < 0.01$) and trophic position ($F_{1,110} = 7.584$, $P < 0.01$, Table 2, Fig. 1). The ww data showed the same trend (ANCOVA, δ^{15}N: $F_{1,110} = 27.917$, $P < 0.01$; trophic position: $F_{1,110} = 21.622$, $P < 0.01$, Table A1). The TMF was 7.8 for the pelagic food web and 3.3 for the benthic food web (Table 2). Overlap in THg between benthic and pelagic upper trophic level species was high (Fig. 1) and lower slope estimates in the benthic food web appeared to be driven by higher THg in the benthic than pelagic primary consumers, i.e., in the predominantly herbivorous grazing amphipod (Hudon, 1983) and limpet (Steneck and Watling, 1982) compared to

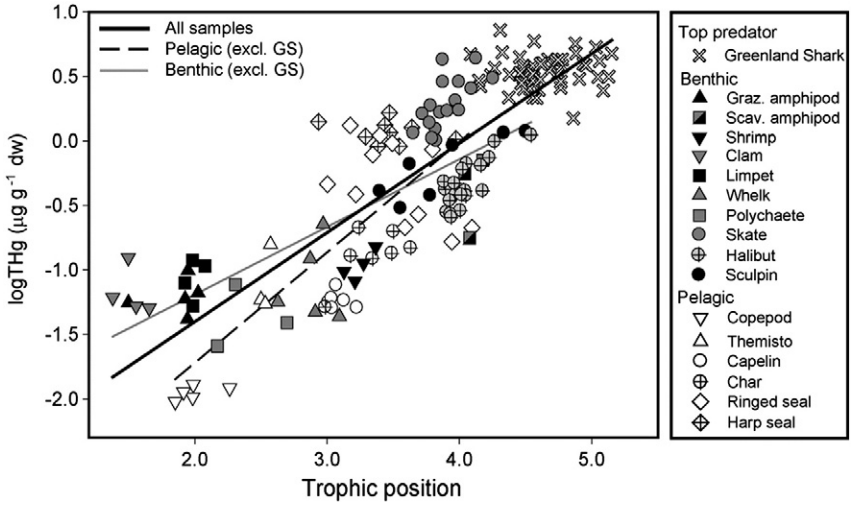

Fig. 1. Ordinary least squares linear regressions of logarithm$_{10}$-transformed THg vs. trophic position for: 1) the entire Cumberland Sound food web ("All samples", heavy black line), 2) pelagic food web components (dashed black line), and 3) benthic food web components (gray line). Greenland Sharks could not be assigned to either the benthic or pelagic food webs and were therefore excluded from the latter two regressions ("excl. GS"). Benthic and pelagic slopes were significantly different based on ANCOVA (see text). All estimated parameters are provided in Table 2.

Table 2
Parameter estimates from Model II (reduced major axes) and simple (ordinary least squares, OLS) linear regressions performed on logarithm$_{10}$-transformed THg ($\mu g \cdot g^{-1}$, dw) and either $\delta^{15}N$ or trophic position (TP) for all Cumberland Sound species ("All samples") and the benthic and pelagic food web components (excluding Greenland Sharks) separately. All slopes had P values <0.001. Trophic magnification factors (TMFs) were calculated from the OLS linear regression slopes. Differences between benthic and pelagic OLS regression slopes were significant based on ANCOVA ($P < 0.05$, see text for details) for both $\delta^{15}N$ and TP.

Food web component	Comparison	Model II		OLS		r^2	TMF
		Slope	Intercept	Slope	Intercept		
All samples ($n = 170$)	$\delta^{15}N$	0.286	−4.535	0.231	−3.712	0.657	4.9
	TP	0.808	−3.222	0.694	−2.795	0.738	
Benthic ($n = 71$)	$\delta^{15}N$	0.194	−3.300	0.154	−2.706	0.626	3.3
	TP	0.661	−2.703	0.525	−2.242	0.632	
Pelagic ($n = 42$)	$\delta^{15}N$	0.397	−6.147	0.290	−4.674	0.531	7.8
	TP	1.220	−4.586	0.892	−3.545	0.534	

copepod (Søreide et al., 2008, Fig. 1). Differences in primary consumer THg (i.e., grazing amphipod = limpet > copepod) were significant based on ANOVA ($F_{2,11} = 77.428$, $P < 0.001$).

3.2. Greenland Shark and prey total mercury, stable isotopes and fatty acids

THg among individual Greenland Sharks did not differ among sampling dates (ANOVA, $P > 0.05$) and was not related to shark $\delta^{15}N$, trophic position, $\delta^{13}C$, length or gender based on the additive model ($P > 0.05$ for all parameters).

The most commonly consumed fish and marine mammal prey by the $n = 51$ Greenland Sharks with stomach contents were (habitat and % occurrence in parentheses): Greenland Halibut (benthic, 52.9%) > ringed seal (pelagic, 29.4%) > Shorthorn Sculpin (benthic, 17.6%) > Arctic Skate (benthic, 15.7%) > harp seal (pelagic, 3.9%) > Arctic Char (pelagic, 0%, although previously observed in the stomachs of other Cumberland Sound Greenland Sharks, B.C. McMeans, pers. obs.) (Table 3). Greenland Sharks had higher THg compared to all six of these fish and marine mammal prey (Fig. 2A) based on ANOVA ($F_{6,121} = 129.32$, $P < 0.001$). THg was higher in Arctic Skate (2.13 ± 1.03 $\mu g \cdot g^{-1}$) and harp seal (1.19 ± 0.24 $\mu g \cdot g^{-1}$) compared to the other prey, but did not differ between these two species (Fig. 2A). The two most commonly consumed prey by Greenland Sharks in the present study, Greenland Halibut (benthic) and ringed seal (pelagic), also did not differ in THg (0.50 ± 0.24 and 0.59 ± 0.39 $\mu g \cdot g^{-1}$, respectively, Fig. 2A). Trophic positions were higher in Greenland Sharks than all prey, and pelagic prey species had lower trophic positions than benthic prey (ANOVA, $F_{6,121} = 73.857$, $P < 0.001$), except that sculpin and ringed seal THg did not significantly differ (Fig. 2B). Values of $\delta^{13}C$ (pair-wise Welch's t tests, $P < 0.05$, Fig. 2C) were higher in Greenland Sharks than prey (except $\delta^{13}C$ was similar among sharks, sculpin and harp seal, $P > 0.05$), but, among prey, only differed between skate and halibut (Fig. 2C). Values of $\delta^{15}N$ on the other hand, were higher in all three benthic compared to pelagic prey species ($F_{6,121} = 46.086$, $P < 0.001$), but did not differ among Greenland Sharks, halibut and sculpin (Fig. 2D).

Neither the first nor the second PC axes extracted from the PCA of shark fatty acids were related to shark THg (OLS linear regressions, $P > 0.05$). PC1 and PC2 extracted from a PCA including a larger set of 15 shark fatty acid proportions (reported in McMeans et al.,

Table 3
Stomach contents of 51 Greenland Sharks, sampled from Cumberland Sound, reported as % occurrence (# of sharks with a given prey · total # of sharks^{-1} * 100).

Prey	% occurrence	Tissue found
Invertebrates		
Buccinum cyaneum	17.6	Whole or operculum
Strongylocentrotus droebachiensis	3.9	Whole
Unidentified squid	9.8	Beaks
Gorgonocephalus arcticus	2.0	Whole
Stegophiura nodosa	5.9	Whole
Unidentified crab	2.0	Pieces of carapace
Shrimp	3.9	Whole
Orchomenella spp., *Onisimus* spp., *Menigrates* spp. (scavenging amphipods)	23.5	Whole
Elasmobranchii		
Somniosus microcephalus	5.9	Pieces of skin and muscle
Amblyraja hyperborea	15.7	Whole or as sections of wing
Teleosts		
Reinhardtius hippoglossoides	52.9	Whole or as pieces of skin and muscle
Myoxocephalus scorpius	17.6	Whole
Lycodes reticulatus	13.7	Whole
Anarichus spp.	7.8	Jaws, skin and muscle
Cyclopteridae	2.0	Whole or skin and muscle
Marine mammals		
Pusa hispida	29.4	Pieces of skin, blubber, muscle or intact seal pups
Phoca groenlandica	3.9	Pieces of skin, blubber, muscle
Erignathus barbatus	3.9	Piece of skin and blubber
Monodon monoceros	2.0	Piece of skin and blubber
Other		
Kelp	3.9	Fragments
Skate egg	3.9	Whole
Unidentified fish	21.6	Pieces of muscle
Unidentified seal	2.0	Pieces of blubber

See Table 1 for common names.

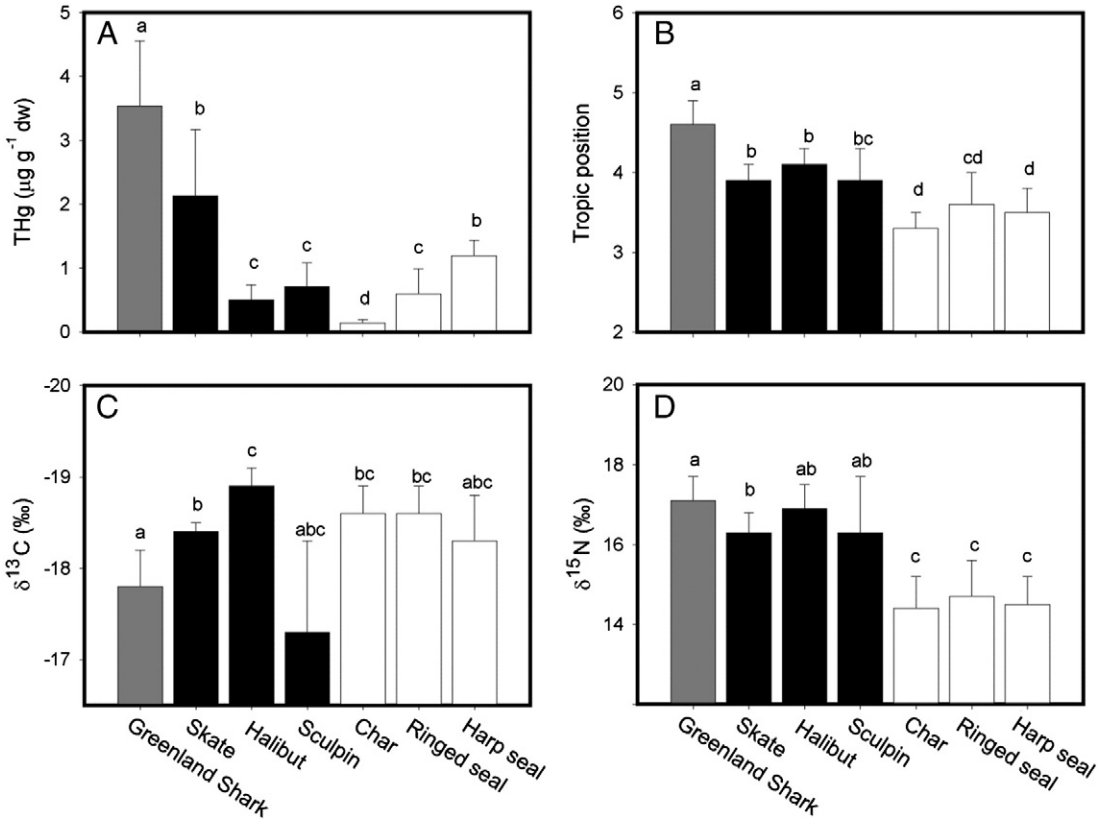

Fig. 2. Mean (SD) of: A. THg, B. trophic position, C. $\delta^{13}C$ and D. $\delta^{15}N$ of Greenland Sharks (gray bars) and benthic (black bars) and pelagic (white bars) prey muscle. Significant differences do not share the same letter (see text for details, THg logarithm$_{10}$ transformed prior to analysis).

2012; McMeans et al., 2012) also did not relate to shark THg ($P > 0.05$). Regressions between shark THg and individual fatty acid proportions revealed that only 18:1n−9 explained a significant, albeit low, amount of the variability in shark THg (Fig. 3A) via the following relationship: $\log_{10}THg = \text{logit}(18{:}1n-9) * 0.373 + 4.707$ ($r^2 = 0.10$, $P < 0.05$). Proportions of 18:1n−9 also increased with shark fork length ($\text{logit}(18{:}1n-9) = \text{length} * 0.001–1.76$, $r^2 = 0.13$, $P < 0.01$) but were not related to shark gender (Welch's t test, $P > 0.05$) or sampling date (ANOVA, $P > 0.05$). The residuals extracted from the shark 18:1n−9 vs. length regression remained positively related to shark THg ($P < 0.05$), indicating that a relationship existed between 18:1n−9 and THg in Greenland Sharks independent of shark fork length.

Comparison of 18:1n−9 (the only fatty acid related to shark THg, see preceding paragraph) among prey revealed differences in the following order: ringed seal = harp seal > Greenland Halibut > Arctic Char > Shorthorn Sculpin = Arctic Skate (ANOVA, $F_{5,57} = 52.99$, $P < 0.0001$, Fig. 3B). Differences in 18:1n−9 proportions among prey (Fig. 3B) were not related to trophic position because ringed and harp seals had higher 18:1n−9 proportions but similar trophic positions to Arctic Char and lower trophic positions than Greenland Halibut, Shorthorn Sculpin and Arctic Skate (Fig. 2B).

4. Discussion

Greenland Sharks in the present study had high THg concentrations that are consistent with their high calculated trophic position and with the observation that THg significantly biomagnified (i.e., increased with trophic position) in the food web of this seasonally ice-covered ecosystem. Basal THg availability differed between habitats (pelagic primary consumers had lower THg) and was likely responsible for higher biomagnification rates ($\log_{10}THg$ vs. $\delta^{15}N$ slopes) in the pelagic than benthic food web. However, these differences at the base of the food webs did not result in consistent differences in THg between known benthic and pelagic Greenland Shark prey. The extent of benthic vs. pelagic feeding by Greenland Sharks in Cumberland Sound is therefore unlikely to consistently impact shark THg exposure. Further, neither Greenland Shark feeding behavior (as inferred from stable isotopes and fatty acids), size, or gender was able to explain intra-specific shark THg variability, except for a positive, but weak, relationship between THg and 18:1n−9. Thus, only biomagnification (based on a significant increase in THg with trophic position from invertebrates to Greenland Sharks), and not individual-level differences in feeding behavior (at least as inferred from stable isotopes and fatty acids) explained the observed THg burdens in Greenland Sharks sampled from Cumberland Sound.

4.1. Food web structure effects on Greenland Shark mercury levels

The significant increase in THg from invertebrates to Greenland Sharks indicates that THg biomagnified in the Cumberland Sound ecosystem. Compared to other Arctic predators, Greenland Shark muscle THg (3.54 ± 1.02 μg·g^{-1}, dw) was similar to muscle THg concentrations of Beaufort Sea estuarine-shelf beluga but lower than epibenthic-associated beluga (2.56 ± 0.80 and 6.53 ± 0.70 μg·g^{-1}, dw, respectively, Loseto et al., 2008a). Greenland Shark liver THg, as previously reported for Cumberland Sound individuals (mean ± SE: 0.49 ± 0.06 μg·g^{-1}, ww; McMeans et al., 2007), was, however, much lower than liver THg of polar bears from the same location (28.30 ± 11.05 μg·g^{-1}, ww; Rush et al., 2008).

The slope of the OLS linear regression of $\log_{10}THg$ vs. $\delta^{15}N$ observed here (0.231) was similar to previous reports (also based on dw THg values) from Beaufort Sea estuarine-shelf (0.255), Amundsen gulf

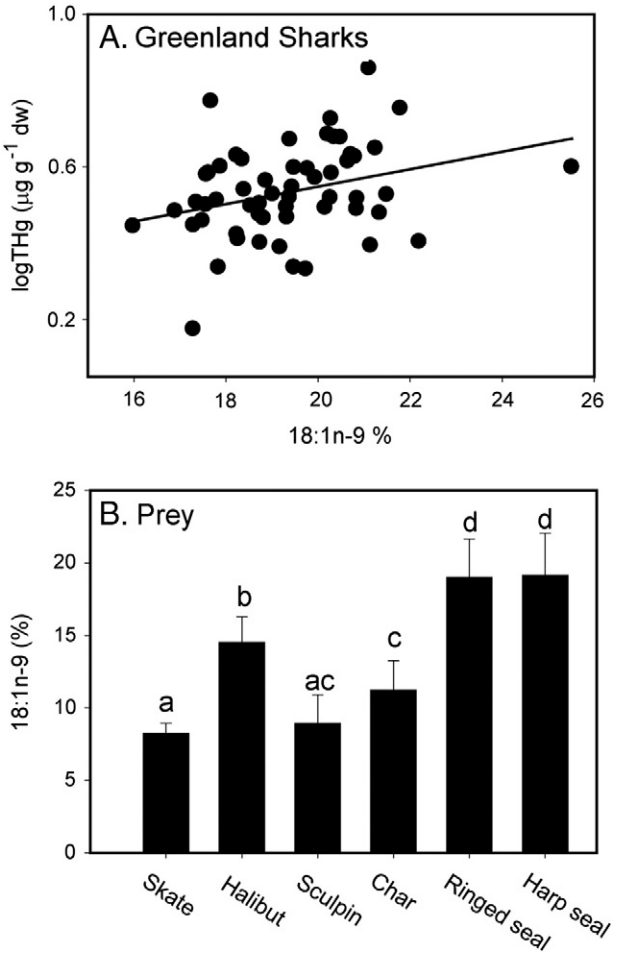

Fig. 3. A. The ordinary least squares linear regression between Greenland Shark logarithm$_{10}$-transformed THg and 18:1n−9 (logit-transformed prior to analysis) which is explained by the following relationship: $\log_{10}\text{THg} = 4.707 + \text{logit}18{:}1\text{n}-9 * 0.373$, $r^2 = 0.10$, $P < 0.05$. B. Proportions of 18:1n−9 (mean ± SD) for several known Greenland Shark prey. Significant differences ($P < 0.05$) based on ANOVA and Tukey's post hoc tests do not share the same letter.

(0.254) and epibenthic (0.232) food webs (Loseto et al., 2008a) but slightly higher than the value of 0.183 reported from Davis Strait (Rigét et al., 2007). Also consistent with previous findings, higher slope estimates were derived from ww than dw THg data (Van der Velden et al., 2013) and, as expected, from Model II than OLS regressions (Quinn and Keough, 2002). The greater ability of trophic position than δ^{15}N to explain THg across the entire food web (based on a higher r^2) also supports previous conclusions that some species have Δ^{15}N values lower than 3.4‰ (seals: Hobson et al., 1996; sharks: Hussey et al., 2010) and that applying a constant Δ^{15}N value across all species and trophic levels is not always appropriate (Hussey et al., 2014). Important considerations regarding our calculated slopes and TMFs are that higher values would be expected if MeHg was analyzed, because MeHg biomagnifies more efficiently than THg and the % contribution of MeHg increases from lower to upper trophic levels (Van der Velden et al., 2013). Including different tissues for vertebrates (e.g., liver instead of muscle) could also have altered our observed TMFs, although it is not clear in which direction, because THg is lower in liver for Greenland Sharks (McMeans et al., 2007), similar to or lower for teleosts (Goldstein et al., 1996), but higher for seals (Wagemann et al., 1998) compared to muscle THg.

Higher THg at the base of the benthic than pelagic food web, but greater THg biomagnification in the pelagic food web, agrees with previous findings (Lavoie et al., 2010). As previously suggested (Lavoie et al., 2010), the greater association of benthos with sediment, a site of Hg methylation (Cossa and Gobeil, 2000), could explain higher THg concentrations in benthic primary consumers (although the water column is increasingly being recognized as an important site of Hg methylation in Arctic waters, Lehnherr et al., 2011). Different TMFs between habitats may have been influenced by different % contributions of MeHg to benthic and pelagic primary consumers (and thus, different Hg transfer efficiencies to higher trophic levels) because trophic position ≈2 marine species can vary from near 0 to almost 100 in their % MeHg (Van der Velden et al., 2013). However, Lavoie et al. (2010) reported higher THg and MeHg (and higher % MeHg) in benthos compared to zooplankton, as well as higher biomagnification slopes in the pelagic than benthic food web for both THg and MeHg, consistent with our findings. The higher rate of THg biomagnification from pelagic primary consumers to higher trophic levels could therefore arise from more linear energy transfer through the pelagic food web, compared to the more reticulate benthic food web (page 56, Fig. 3.8 AMAP, 2011; McMeans et al., 2013b). THg biomagnification rates do not always differ among Arctic habitats (Loseto et al., 2008a; Van der Velden et al., 2013), however, and more work is clearly needed to identify what mechanism(s) drive both similarities and differences in THg bioavailability and biomagnification rates within and among Arctic ecosystems (but see Lavoie et al., 2013 for a synthesis of possible drivers of variation in global THg biomagnification rates). Importantly, the strength of the Hg–δ^{15}N relationship across Arctic regions, regardless of habitat or location, does indicate that it may be a useful tool for identifying trophic linkages and which species fit in a certain food web (Foster et al., 2012).

The habitat-related differences in THg basal availability and rates of biomagnification observed here (see preceding paragraph) did not translate into consistent differences between benthic and pelagic prey of Greenland shark. For example, Greenland Halibut and Arctic Skate share a benthic habitat in Cumberland Sound but had significantly different muscle THg levels. Polychlorinated biphenyl concentrations (Σ of 89 PCB congeners) were also higher in Cumberland Sound Arctic Skate ($n = 5$, range = 202 to 2652, mean ± SD = 1388 ± 10.34 ng·g^{-1} lipid weight) compared to Greenland Halibut ($n = 8$, range = 146 to 445, mean ± SD = 218 ± 96 ng·g^{-1} lipid weight) (McKinney et al., 2012). The reasons for such high contaminant concentrations in Arctic Skate are unclear. The two seal species sampled in the present study also had different THg (ringed < harp seal), even though both generally consume diets dominated by invertebrates and fish (McMeans et al., 2013b and references therein) and had similar calculated trophic positions (Fig. 2). This may reflect the consumption of more contaminated prey from outside of Cumberland Sound by transient harp seals, compared to resident ringed seals (McKinney et al., 2012). Alternatively, the two most commonly consumed prey of Greenland Sharks (Greenland Halibut and ringed seal) differed in their habitat (benthic and pelagic, respectively) but not their THg. High THg variability among upper trophic level species has been previously noted (Atwell et al., 1998), and species-specific characteristics not assessed here, including growth rate and Hg elimination rate, could explain observed inter-specific THg differences. The analysis of MeHg and multiple tissues, for example, would allow more insight into possible inter-species differences in Hg tissue allocation and elimination processes (Bjerregaard et al., 2011). Additional data are required to address these ideas. However, the lack of consistent differences in THg between benthic and pelagic prey suggests that habitat-related differences in THg availability or biomagnification rates will not consistently impact THg exposure to Cumberland Sound Greenland Sharks.

4.2. Mercury relationships with Greenland Shark feeding behavior

Individual Greenland Shark feeding behavior as inferred from δ^{15}N, δ^{13}C and fatty acids could not robustly explain intra-specific THg

variability. One exception was a weak but positive relationship between THg and 18:1n − 9, which could indicate greater exposure to some individual sharks via greater seal consumption (due to higher proportions of this fatty acid in seals compared to teleost prey). However, significant positive THg relationships with the other seal fatty acids (16:1n − 7, 22:5n − 3), and negative relationships with fatty acids that are lower in seals (e.g., 22:1n − 11) would make this possibility more convincing, especially because 18:1n − 9 can arise from metabolism, not diet, in fish (e.g., via desaturation from 18:0 or chain shortening of C22 and C20 fatty acids; Tocher, 2003). Greenland Sharks also did not exhibit gender- or size-related feeding in a manner that influenced THg concentrations, at least within the size ranged sampled (fork length range: 209 to 345 cm). Previous studies also found no evidence to support a gender or size effect on Greenland shark hepatic THg (fork length range: 234 to 322 cm, McMeans et al., 2007) or organic contaminant levels (fork length range: 250 to 325 cm, Fisk et al., 2002). It is possible that future work may uncover an effect of length if a larger size range was obtained, which included individuals at the higher end of the Greenland Shark's maximum known size (>600 cm, Bigelow and Schroeder, 1948).

Contrary to our findings for Greenland Sharks, THg was significantly higher in larger than smaller beluga (Loseto et al., 2008b), in female than male polar bears (St. Louis et al., 2011), and in individual polar bears with higher $\delta^{15}N$ and lower $\delta^{13}C$ (Cardona-Marek et al., 2009). The lack of these relationships in the present study could indicate that Greenland Sharks did not maintain individual-level variation in prey selection, at least not long enough to drive relationships between biological (size, gender) and ecological (stable isotopes, fatty acids) variables and THg. Additional data are needed to determine the extent of prey selection by individual Greenland Sharks. However, the presence of multiple prey types in several shark stomachs (the number of sharks with stomachs that contained 1, 2, 3, 4, 5, 6 and 7 different prey species was 7, 6, 12, 2, 6, 4 and 2) and scavenging amphipods in 23.5% of shark stomachs (Table 3) is consistent with a generalist and opportunistic feeding strategy for some individuals. Additional possibilities are that prey selection and feeding behavior influences on Greenland Shark THg were not observable from our data due to: 1) THg overlap among dominant prey species (Fig. 2), or 2) different turnover times between ecological tracers and THg (Gaden et al., 2009). Sampling of multiple tissues (particularly fast-turnover tissues like blood) for THg and MeHg (and stable isotope) analysis in sharks and prey, and a greater understanding of whether individual fatty acids arise from dietary or metabolic processes (e.g., from ^{13}C fatty acid analysis) would help better link intra-specific THg variability with feeding behavior in Greenland Sharks.

Regardless of the reasons for intra-specific variation among Greenland Sharks in Cumberland Sound, our findings indicate that this species, given its large size and abundance, could significantly contribute to the biotic THg pool in northern seas. Based on THg concentrations for Greenland Shark muscle (this study) and liver (McMeans et al., 2007), we estimate that over 200 mg of THg may be present in the combined muscle and liver of a single Greenland Shark (see Appendix 1 for a full description of this calculation). Based on historical catches of tens of thousands of individuals in Greenland waters (MacNeil et al., 2012), 10,000 Greenland Sharks could feasibly inhabit Greenland and surrounding waters, and would contain over 2000 g of THg.

Important considerations for our study are that we sampled one tissue (muscle) for Greenland Sharks and prey, and not whole body burdens. Finally, it must be recognized that Greenland Sharks are mobile (Campana et al., in press; Fisk et al., 2012) and sampling prey from a wider range of ecosystems may lend better insight into the possible sources of THg to Greenland Sharks throughout the Arctic.

5. Conclusion

Greenland Sharks had high muscle THg values that were consistent with biomagnification and within the previously reported range for some warm-blooded Arctic predators (e.g., beluga). Greenland Sharks should therefore be included in future THg modeling and monitoring efforts because they are likely a large sink for THg contained within the biotic pool in northern seas, especially given their large size and possibly high abundance (MacNeil et al., 2012). Our findings additionally indicate that because Greenland Sharks consume a wide range of prey (based on stomach contents) they are likely involved in a variety of THg trophic transfer pathways in both benthic and pelagic habitats. Although additional work is needed to explain intra-specific THg variability in Greenland Sharks, our results suggest that either increases in basal THg levels (that would be transported up the food web due to observed THg biomagnification) or increases in the abundance or availability of highly THg-contaminated species (harp seal and Arctic Skate had the highest muscle THg concentrations of the prey species sampled) are avenues by which climate change could cause increased THg burdens in Greenland Sharks.

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Appendix 1

Estimating the mass of THg in the combined muscle and liver of Greenland Sharks.

We cannot estimate total THg body burden, but have the THg and mass data to estimate how much THg would be contained in the muscle and liver of an individual Greenland shark. The mass of a Greenland Shark that is 273 cm in fork length (292 cm in total length, the mean length of sharks sampled in the present study) is 262 kg based on the following length and mass relationship provided by MacNeil et al. (2012): $\ln(\text{Mass}) = -12.2 + 3.13 * (\ln(\text{Total Length}))$. The liver mass of a shark this size would be approximately 30 kg based on total body and liver masses recorded from Svalbard Greenland Sharks (K. Kovacs, C. Lydersen, A.T. Fisk, unpub. data). No estimates for muscle weight as a function of total body weight were available for Greenland Sharks. However, the dressed weight (i.e., carcass without head, tail, fins, gills or guts) of a 273 cm fork length shark would be 120 kg based on the following fork length and dressed weight relationship for *Sphyrna* spp. (García-Cortés and Mejuto, 2002): Dressed Weight $= 9.95 \times 10^{6} * \text{Fork Length}^{2.91}$. The relationship for *Sphyrna* spp. was used because the other sharks included in García-Cortés and Mejuto (2002) were smaller than 273 cm fork length. The dressed weight estimate does, however, include cartilage mass and is thus an overestimate for muscle mass alone. For reference, after removing the liver mass, the dressed weight estimate of 120 kg is approximately half of the remaining Greenland Shark body mass [i.e., $(262–30\ \text{kg}) * 2^{-1} = 116\ \text{kg}$].

Given the mean wet weight THg of Greenland Shark: 1) muscle from the present study ($1.62\ \mu g \cdot g^{-1} = mg \cdot kg^{-1}$), and 2) liver from McMeans et al. (2007) ($0.49\ \mu g \cdot g^{-1} = mg \cdot kg^{-1}$), 209 mg of combined THg would be present in the muscle ($120\ kg * 1.62\ mg \cdot kg^{-1}$ THg ww = 194 mg) and liver ($30\ kg * 0.49\ mg \cdot kg^{-1}$ THg ww = 14.7 mg) of a Greenland Shark that is 292 cm total length. This means that the combined muscle and liver of every ten thousand Greenland Sharks could contain 2090 g of THg.

Table A1
Wet weight (ww) THg parameter estimates from Model II (reduced major axes) and ordinary least squares (OLS) linear regressions performed on individual values of $\delta^{15}N$ and trophic position (TP) vs. logarithm$_{10}$-transformed THg ($\mu g \cdot g^{-1}$, ww) for all Cumberland Sound species. Regressions were performed on either the entire food web ("All samples"), benthic species only or pelagic species only (Greenland Sharks were excluded from the latter two groups). The amount of variation explained by the OLS linear regression (r^2) is shown. All slopes differed significantly from zero at $\alpha = 0.05$. Based on ANCOVA, the pelagic food web had significantly higher slopes than the benthic food web for both $\delta^{15}N$ and trophic position (see text for details).

Food web component	Comparison	Model II regression		OLS regression		r^2	P
		Slope	Intercept	Slope	Intercept		
All samples ($n = 170$)	logTHg ww vs. $\delta^{15}N$	0.335	−5.807	0.273	−4.858	0.662	<0.001
	logTHg ww vs. TP	0.947	−4.267	0.827	−3.816	0.762	<0.001
Benthic ($n = 71$)	logTHg ww vs. $\delta^{15}N$	0.196	−3.939	0.164	−3.471	0.699	<0.001
	logTHg ww vs. TP	0.666	−3.337	0.560	−2.975	0.705	<0.001
Pelagic ($n = 42$)	logTHg ww vs. $\delta^{15}N$	0.480	−7.878	0.377	−6.471	0.617	<0.001
	logTHg ww vs. TP	1.474	−5.993	1.148	−4.960	0.607	<0.001

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