Diet and resource use among Greenland sharks (*Somniosus microcephalus*) and teleosts sampled in Icelandic waters, using δ^{13}C, δ^{15}N, and mercury

Bailey C. McMeans, Jörundur Svavarsson, Susan Dennard, and Aaron T. Fisk

Abstract: Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes and total mercury (Hg) were used to investigate diet and resource use among Greenland sharks (*Somniosus microcephalus*) and 14 teleosts inhabiting Icelandic waters. Greenland shark stomachs contained 11 of the teleosts sampled, along with other fishes and marine mammal tissues. Teleost resource use ranged from pelagic (e.g., *Argentina silus*) to benthic (e.g., *Anarhichas lupus*) based on δ^{13}C, and relative trophic positions (TP, based on δ^{15}N) ranged from 3.0 (*Mallotus villosus*) to 3.8 (e.g., *Brosme brosme*). Greenland shark δ^{13}C indicated feeding on benthic and pelagic resources, with a high input of pelagic carbon, and δ^{15}N indicated a relative TP of 4.3. Log[Hg] increased with δ^{15}N (i.e., TP) from teleosts to Greenland sharks and was higher in offshore vs. inshore teleosts. Linear regressions revealed that log[Hg] was better described by both δ^{15}N and δ^{13}C-assigned resource use than by δ^{15}N alone. Hg was useful for supporting the TPs suggested by δ^{15}N, and the higher Hg in offshore fishes could help explain the high Hg of Greenland sharks. Results from this study demonstrated the potential use of Hg as a dietary tracer in marine fishes.

Résumé : Les isotopes stables de carbone (δ^{13}C) et d'azote (δ^{15}N) et le mercure total (Hg) nous ont servi à étudier le régime alimentaire et l'utilisation des ressources chez la laimargue atlantique (*Somniosus microcephalus*) et 14 téléostéens habitant les eaux islandaises. Les estomacs de laimargues atlantiques contenaient 11 des téléostéens échantillonnés, ainsi que des tissus d'autres poissons et de mammifères marins. L'utilisation de la ressource de téléostéens comprenait des poissons de pélagiques (par ex., *Argentina silus*) à benthiques (par ex., *Anarhichas lupus*) d'après δ^{13}C et leurs positions trophiques relatives (TP, basée sur δ^{15}N) variaient de 3,0 (*Mallotus villosus*) à 3,8 (par ex., *Brosme brosme*). Le δ^{13}C des laimargues atlantiques indique qu'elles se nourrissent de ressources benthiques et pélagiques, avec un apport élevé de carbone pélagique et leur δ^{15}N indique une TP relative de 4,3. Log[Hg] augmente en fonction de δ^{15}N (c'est-à-dire la TP) des téléostéens aux laimargues atlantiques et est plus élevé chez les téléostéens du large que chez ceux de la côte. Des régressions linéaires montrent que log[Hg] est mieux décrit par l'utilisation des ressources assignées à la fois par δ^{15}N et δ^{13}C que par δ^{15}N seul. Le Hg est utile pour appuyer les TP indiquées par δ^{15}N et les concentrations plus élevées de Hg dans les poissons du large pourraient aider à expliquer les fortes concentrations de Hg dans les laimargues atlantiques. Les résultats de notre étude démontrent l'utilité potentielle de Hg comme traceur alimentaire chez les poissons marins.

[Traduit par la Rédaction]

Introduction

Knowledge concerning the diet of marine fish is important for understanding energy and contaminant flow among predators and prey and for an ecosystem-based approach to fisheries management. Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) are frequently used in ecological studies because they can provide information about resource use (e.g., benthic vs. pelagic feeding) and trophic position (TP) of marine fish, respectively (Davenport and Bax 2002; Fisk et al. 2002; Sherwood and Rose 2005). The application of δ^{13}C and δ^{15}N has increased understanding of marine food web structure, although several issues can confound their interpretation. For example, overlapping δ^{13}C values among consumers can prevent the differentiation of feeding behaviors (Davenport and Bax 2002; Cai et al. 2007), and spatial variability in δ^{13}C and δ^{15}N can result in erroneous identification of resource use and TP (Vander Zanden and Rasmussen 1999). For the latter issue, adequate sampling of baseline organisms can account for spatial variability in δ^{13}C and δ^{15}N (Vander Zanden and Rasmussen 1999; Post 2002). However, the former issue remains troublesome, especially in mobile, upper TP consumers that use multiple resources (Cai et al. 2007).

The combination of certain contaminants with δ^{13}C and δ^{15}N values can provide additional information about the diet of fish (Fisk et al. 2002; Bank et al. 2007). Mercury (Hg), for example, is predominantly driven by diet in fish

B.C. McMeans,[1] S. Dennard, and A.T. Fisk. Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4, Canada.
J. Svavarsson. Institute of Biology, University of Iceland, Sturlugata 7, IS-101 Reykjavik, Iceland.

[1]Corresponding author (e-mail: mcmeans@uwindsor.ca).

(Harris and Bodaly 1998), increases with TP (indicated by $\delta^{15}N$; Kidd et al. 1995), and can differ among fish that use different resources (indicated by $\delta^{13}C$; Power et al. 2002). If Hg differs among fish that feed on different resources and (or) at a higher TP as suggested by previous studies, then Hg could be useful for providing additional information about the diet of marine fish. For example, higher Hg in grey snapper (*Lutjanus griseus*) vs. red snapper (*Lutjanus campechanus*) sampled from the Gulf of Mexico was used to indicate that grey snapper fed on more pelagic prey and at a slightly higher TP — a contention that was supported by previous diet data (Bank et al. 2007). Although variables other than diet (e.g., length, age, and activity costs) can influence fish Hg concentrations (e.g., Trudel and Rasmussen 2006), the ability of Hg to separate fishes based on TP and resource use indicates the potential of Hg as a tracer in ecological studies.

The marine environment surrounding Iceland supports several species of commercially important fishes (e.g., Atlantic cod, *Gadus morhua*), as well as the megafaunal vertebrate the Greenland shark, *Somniosus* (*Somniosus*) *microcephalus*. Greenland sharks are rarely included in food web studies, and few data exist regarding their biology and (or) ecology. Only one previous study has assessed the feeding ecology of Greenland sharks using stable isotopes (Fisk et al. 2002), and no study has investigated the diet of Greenland sharks inhabiting Icelandic waters. The Icelandic fishery presents an opportunity to sample both Greenland sharks, which are incidentally caught as bycatch, and their potential teleost prey for $\delta^{13}C$ and $\delta^{15}N$ analysis. Identifying important energy sources to Greenland sharks requires the ability to differentiate resource use among their prey. However, some teleosts inhabiting Icelandic waters can use similar resources based on previous stomach content (e.g., Jaworski and Ragnarsson 2006) and stable isotope data (Sarà et al. 2009). For example, a recent study reported that Atlantic cod, haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), and ling (*Molva molva*) sampled in the waters surrounding Iceland had similar $\delta^{13}C$ values (Sarà et al. 2009). Hg could be useful for more clearly characterizing the feeding behavior of Greenland sharks and their potential teleost prey in Icelandic waters. The objective of this study was to identify resource use (i.e., benthic vs. pelagic feeding) and TPs among Greenland sharks and 14 teleost species sampled from Icelandic waters using $\delta^{13}C$, $\delta^{15}N$, and Hg. Greenland shark stomach contents were also identified and used to calculate species-specific discrimination factors ($\Delta^{13}C$ and $\Delta^{15}N$).

Materials and methods

Sampling of Iceland fishes

Greenland sharks (n = 22; 3 males, 19 females) were collected during November 2001 – August 2005 as bycatch via longline or trawl net in Icelandic waters (Fig. 1) and were measured for total length (TL) (Table 1). Approximately 6 g of muscle from under each shark's first dorsal fin (n = 19; 3 males, 16 females) was sampled for $\delta^{13}C$, $\delta^{15}N$, and Hg analyses. Shark stomach contents were identified as close to species level as possible, counted, and weighed (wet weight) (Table 2).

The remainder of species were collected as part of the Icelandic fishery using fishing nets (for species names and sampling depths, see Table 1), except for glacial eelpout (*Lycodes glacialis*) and deepwater shrimp (*Bythocaris leucopis*), which were sampled by an Agassiz trawl. All teleosts were collected during August – November 2005, except for capelin, glacial eelpout, and deepwater shrimp, which were sampled during January – April 2007. Two groups of redfish were sampled: (*i*) inshore redfish (*Sebastes marinus*) and (*ii*) offshore redfish (*Sebastes marinus* (n = 3) and *Sebastes mentella* (n = 3)). Because *S. marinus* and *S. mentella* are closely related and have similar diets of pelagic zooplankton (Jaworski and Ragnarsson 2006; Petursdottir et al. 2008), all *Sebastes* spp. collected inshore were labeled as "inshore redfish" and all *Sebastes* spp. collected offshore were labeled as "offshore redfish" (Fig. 1; Table 1). All fish were measured for TL (Table 1) and approximately 4 g of muscle from the left flank (the left flank was arbitrarily chosen) of each individual was sampled for $\delta^{13}C$, $\delta^{15}N$, and Hg analyses. Because of their small size, capelin were analyzed whole. Muscle of deepwater shrimp was sampled for stable isotope and Hg analysis. Weights were not recorded because most fish were gutted prior to sampling.

Teleosts were categorized into those sampled inshore (i.e., Atlantic cod, haddock, saithe, wolffish, European plaice, lemon sole, and inshore redfish; sampling area depicted by box on Fig. 1) and those sampled offshore (i.e., greater argentine, capelin, blue ling, ling, tusk, offshore redfish, and glacial eelpout) (Fig. 1). Greenland sharks were predominantly collected offshore, although four individuals were captured within 50 km of the Icelandic coast (Fig. 1).

Stable isotope analysis

Stable isotopes are expressed as delta (δ) values using the following equation:

$$(1) \qquad \delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is ^{15}N or ^{13}C and R is the ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. The isotope ratios are expressed relative to the international standard PDB (Pee Dee Belemnite) and atmospheric N_2 for carbon and nitrogen samples, respectively. For $\delta^{13}C$ and $\delta^{15}N$ analysis, muscle was subsampled into approximately 2 g batches, freeze-dried for 48 h, and then homogenized using a ball mill grinder (SPEX CertiPrep 8000-D ball milling unit, SPEX CertiPrep, Metuchen, New Jersey). Capelin were freeze-dried whole prior to homogenization and then were subsampled. The presence of lipids in shark and fish muscle samples can negatively skew observed $\delta^{13}C$ values (Post et al. 2007); thus, lipids were removed from all samples prior to stable isotope analysis following a modified method outlined by Bligh and Dyer (1959) as follows: 5 mL of 2:1 chloroform–methanol was added to homogenized samples, samples were vortexed for 30 s, allowed to sit for 24 h, and then centrifuged, and the solution was then decanted through filter paper into preweighed aluminum trays for gravimetric determination of lipids. Approximately 2 mg of tissue was weighed into tin capsules, and $\delta^{13}C$ and $\delta^{15}N$ were determined on a continuous-flow isotope ratio mass spectrometer (Finnigan MAT Delta[plus], Thermo Finnigan, San Jose, California) coupled with an element analyzer (Costech, Valencia, California). The precision of the isotopic

1430

Can. J. Fish. Aquat. Sci. Vol. 67, 2010

Fig. 1. Sampling locations for invertebrates and fishes from Icelandic waters. The rectangle indicates the sampling area for the following species: Atlantic wolffish, lemon sole, saithe, haddock, European plaice, Atlantic cod, and inshore redfish. Deepwater shrimp were sampled in the same location as glacial eelpout. See Table 1 for species names.
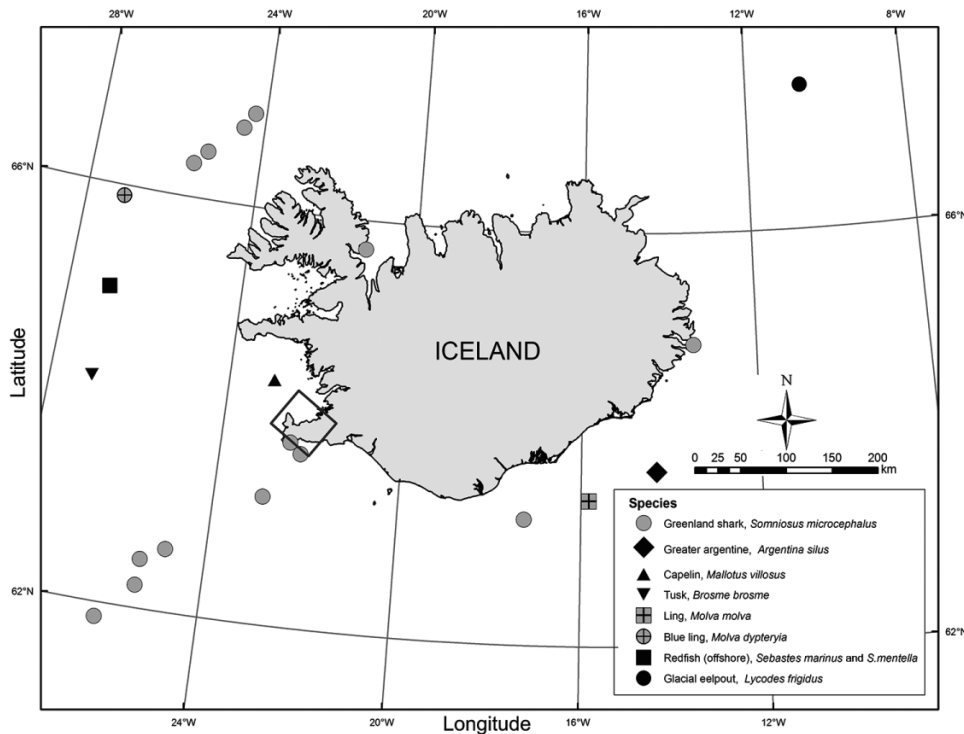

Table 1. Sample number (*n*), trophic position (TP), mean ± 1 standard error (SE) of $\delta^{15}N$ (‰), $\delta^{13}C$ (‰), total mercury (Hg) (µg·g^{-1}, dry weight), and length (cm), and sampling depth (m, provided as a range where necessary) for species sampled in Icelandic waters.

Species	*n*	TP	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	Hg (µg·g dry weight^{-1})	Length (cm)	Depth (m)
Invertebrates							
Deepwater shrimp, *Bythocaris leucopis*	6	2.0	13.5±0.1	−17.1±0.7	<DL		2002
Chondricthyes							
Greenland shark, *Somniosus microcephalus*	19	*4.3*[a]	15.3±0.2	−17.8±0.3	5.93±0.59	415.6±25.2	73–740
Teleostei							
Greater argentine, *Argentina silus*	6	*3.2*	10.8±0.3	−18.6±0.2	0.20±0.05	37.3±4.6	382
Capelin, *Mallotus villosus*	10	*3.0*	10.1±0.2	−19.9±0.1	<DL	14.4±1.0	
Atlantic cod, *Gadus morhua*	5	3.7	11.8±0.2	−16.6±0.1	0.18±0.04	62.4±9.1	40
Haddock, *Melanogrammus aeglefinus*	7	3.6	11.6±0.1	−16.2±0.1	0.16±0.04	60.6±4.7	37
Saithe, *Pollachius virens*	11	3.4	11.0±0.2	−16.7±0.1	0.12±0.01	42.5±2.7	40
Tusk, *Brosme brosme*	6	3.8	12.7±0.4	−16.7±0.1	1.70±0.09	38.4±13.9	373
Ling, *Molva molva*	6	3.6	12.0±0.2	−17.1±0.1	0.89±0.09	87.2±11.9	232
Blue ling, *Molva dypteryia*	5	3.8	13.0±0.1	−17.7±0.1	0.94±0.19	79.0±5.6	525
Atlantic wolffish, *Anarhichas lupus*	5	3.1	9.7±0.3	−15.2±0.1	0.39±0.06	51.6±2.7	110
European plaice, *Pleuronectes platessa*	6	3.2	10.2±0.4	−15.2±0.2	0.12±0.01	42.8±5.6	110
Lemon sole, *Microstomus kitt*	6	3.5	11.2±0.5	−15.4±0.1	0.25±0.08	32.0±3.0	60
Redfish (inshore), *Sebastes marinus*	6	3.6	11.5±0.3	−16.7±0.3	0.37±0.07	36.3±2.2	40
Redfish (offshore), *S. marinus* and *S. mentella*	6	*3.2*	11.0±0.2	−19.2±0.2	0.72±0.17	35.5±4.7	275
Glacial eelpout, *Lycodes frigidus*	9	3.4	14.8±0.2	−19.3±0.3	1.21±0.13	40.8±7.2	1487–2108

Note: The TP of glacial eelpout was calculated using *Bythocaris leucopis* $\delta^{15}N$ as a baseline, and TPs of the remaining offshore and inshore species were calculated using the $\delta^{15}N$ of *Argentina silus* (TPs in italic type) and *Pleuronectes platessa* (TPs in Roman type) as a baseline, respectively. Species with Hg concentrations below detection limit are indicated by "<DL."

[a]Species-specific $\Delta^{15}N$ of 4.0‰ used in Greenland shark TP calculation, see eq. 2 in Materials and methods for $\Delta^{15}N$ calculation.

Table 2. Stomach contents for 22 individual Greenland sharks sampled off the coast of Iceland.

Prey species	Total no.	Percent frequency	W_i (kg)	P_i (%)
Great laternshark, *Etmopterus princeps*	1	4.5	0.2	
Starry ray, *Raja radiate*	2	4.5	3	
Rat-fish, *Chimera monstrosa*	2	4.5	n/d	
Teleostei (unidentified teleosts)	13	27.3	7.5	
Atlantic herring, *Clupea harengus*	9	4.5	4.5	
Greater argentine, *Argentina silus*	14	18.2	8.9	1.57
Lantern fish, *Myctophidae* sp.	5	4.5	n/d	
Atlantic cod, *Gadus morhua*	60	22.7	116	20.47
Haddock, *Melanogrammus aeglefinus*	2	9.1	1.5	0.26
Saithe, *Pollachius virens*	13	27.3	31	5.47
Tusk, *Brosme brosme*	2	9.1	2	0.35
Ling, *Molva molva*	4	9.1	2	0.35
Lotidae (unidentified ling, blue ling, tusk)	36	22.7	64	11.30
Atlantic wolffish, *Anarhichas lupus*	6	18.2	10.2	1.80
Spotted wolffish, *Anarhichas minor*	1	4.5	1	
Pleuronectidae (unidentified flatfish)	2	9.1	0.8	
European plaice, *Pleuronectes platessa*	10	4.5	6	1.06
Dab, *Limanda limanda*	4	9.1	2.2	
Halibut, *Reinhardtius hippoglossoides*	1	4.5	4	
Lumpsucker, *Cyclopterus lumpus*	4	4.5	2	
Redfish, *Sebastes* spp.	303	54.5	325	57.36
Mammalia (unidentified mammal)	F	4.5	20	
Unidentified pinniped	Head, F, F	13.6	23	
Unidentified dolphin or porpoise	F, F, F	13.6	100.7	
Polar bear, *Ursus maritimus*	Leg, skin	4.5	4	

Note: Four shark stomachs were empty. Marine mammal tissue was found as fragments (F) of skin, blubber, and (or) muscle except where indicated. "Total no." is the number of individuals of each prey species found in all stomachs. Percent frequency is the number of shark stomachs in which each prey species was found, divided by total number of stomachs quantified. W_i is the total weight (kg) of all individuals of each prey species from all stomachs, and "n/d" indicates no data. Diet proportions (P_i, reported as %) are provided for teleosts that were analyzed for δ^{13}C and δ^{15}N in the present study. P_i is equal to W_i/W_{tot}, where W_{tot} is 566.6 kg and is equal to the total weight (kg) of the 10 prey for which stable isotopes were analyzed. δ^{13}C and δ^{15}N for offshore redfish were used for "Redfish, *Sebastes* spp." and the mean δ^{13}C and δ^{15}N for ling, blue ling, and tusk were used for "Lotidae." δ^{13}C and δ^{15}N values are provided in Table 1.

analyses was <0.15‰ for δ^{13}C and δ^{15}N based on internal reference samples.

Mercury analysis

Total Hg in muscle of deepwater shrimp and fishes and whole capelin was analyzed by atomic absorption spectrometry vapor generation at the Great Lakes Institute for Environmental Research, University of Windsor (Windsor, Ontario, Canada), which is accredited by the Canadian Association of Environmental Analytical Laboratories. To ensure accuracy, 20% of samples run were blanks, replicates, and National Research Council Canada standards (Dorm-2, Dolt-3). All Hg concentrations are reported in µg·g dry weight (dw)$^{-1}$, and the detection limit was 0.05 µg·g dw^{-1} (three times the standard deviation (SD) of blanks).

Although total Hg was analyzed, >90% of the Hg in fish is in the form of methylmercury (Becker and Bigham 1995), and total Hg is often used as a proxy for methylmercury (Power et al. 2002; Chumchal et al. 2008).

Data analysis

Among all individuals of all species sampled (n = 131), three outliers based on δ^{15}N and δ^{13}C were identified using

probability plots and were removed from all analyses. Values of δ^{15}N and δ^{13}C were normally distributed based on probability plots, and Hg data was log$_{10}$-transformed prior to inclusion in statistical models and is referred to as "log[Hg]". Species means of δ^{15}N, δ^{13}C, and log[Hg] were considered significantly different if their 95% confidence intervals (CIs) did not overlap (95% CIs are shown in Figs. 2 and 3). Comparing 95% CIs is a conservative method for identifying differences between means (Payton et al. 2003) and provided a straightforward way to compare variables among the 15 species sampled in the present study. However, comparing 95% CIs among species suffers from the issue of increased type I error rate due to multiple comparisons.

Isotope discrimination factors (Δ^{13}C and Δ^{15}N) were calculated for Greenland sharks based on equations from Sherwood and Rose (2005) as follows, using δ^{15}N as an example:

$$(2) \qquad \Delta^{15}N = \delta^{15}N_{shark} - \sum(P_i \cdot \delta^{15}N_i)$$

where $\delta^{15}N_{shark}$ is the mean δ^{15}N of Greenland sharks and $\delta^{15}N_i$ is the mean δ^{15}N of the ith prey species. P_i is equal to the ratio of the total weight (kg) of prey i consumed by all sharks (W_i) to the total weight (kg) of all prey (W_{tot}) (Table 2).

1432

Can. J. Fish. Aquat. Sci. Vol. 67, 2010

Fig. 2. Mean ± 95% confidence intervals of δ13C (‰) and δ15N (‰) for species sampled from Icelandic waters. Symbols indicate the δ13C-assigned resource use category for each teleost species as follows: offshore pelagic (solid symbols), offshore mixed (symbols with dark shading), inshore mixed (symbols with light shading), and inshore benthic (open symbols).
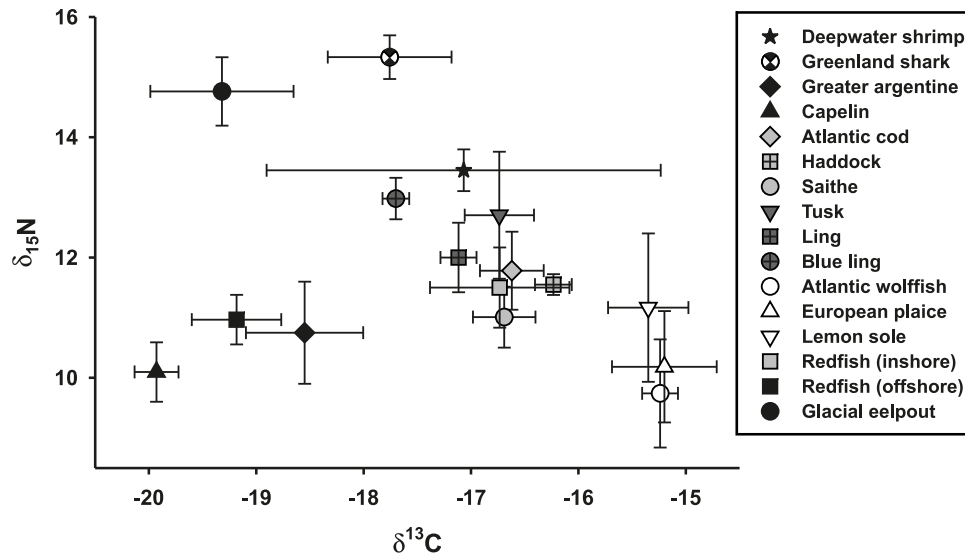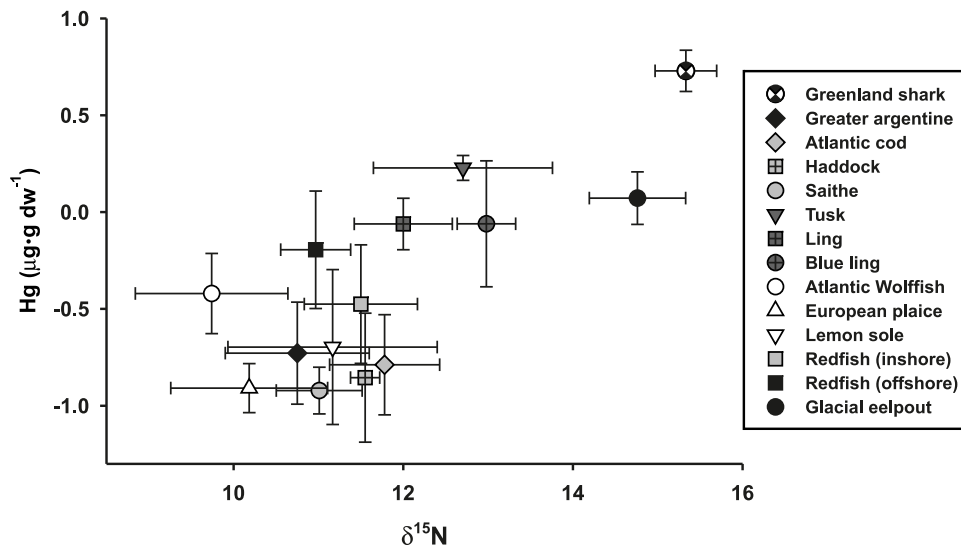

Fig. 3. Mean ± 95% confidence intervals of δ15N (‰) vs. log10-transformed total mercury (Hg) for species sampled from Icelandic waters. Symbols indicate the δ13C-assigned resource use category for each teleost species as follows: offshore pelagic (solid symbols), offshore mixed (symbols with dark shading), inshore mixed (symbols with light shading), and inshore benthic (open symbols).

Habitat and resource use can be identified in marine fish using δ13C because benthic-feeding consumers are typically more enriched in 13C relative to pelagic-feeding consumers (Davenport and Bax 2002; Sherwood and Rose 2005). Icelandic teleosts were assigned to one of four groups referred to as "resource use categories" based on significant differences (i.e., 95% CI) in δ13C and sampling location (i.e., inshore vs. offshore). Trophic positions were calculated for Icelandic species using δ15N as follows:

$$(3) \quad TP = TP_{baseline} + (\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/\Delta^{15}N$$

where $TP_{baseline}$ is the estimated TP of the baseline organism, $\delta^{15}N_{consumer}$ and $\delta^{15}N_{baseline}$ are the mean δ15N of the consumer of interest and of the baseline organism, respectively, and 3.4‰ was used as the $\Delta^{15}N$ for teleosts (Post 2002). The $\Delta^{15}N$ calculated for Greenland sharks using eq. 2 was included in the calculation of Greenland sharks' TP in place of 3.4‰. Mean δ15N of deepwater shrimp, which were assigned a TP of 2.0, was used as the baseline for glacial eelpout. Greater argentine and European plaice were used as baselines for the remaining species sampled offshore and inshore, respectively. Greater argentine and European plaice

Table 3. Resource use based on $\delta^{13}C$ for teleosts sampled in Icelandic waters and stomach content data from previously published studies.

Species	$\delta^{13}C$ resource	Previous diet data		
		Predominant prey items	Size (cm)	Reference
Greater argentine, *Argentina silus*	Pelagic	Euphausiacea, Amphipoda	n/d	Scott and Scott 1988
Capelin, *Mallotus villosus*	Pelagic	*Calanus finmarchius, C. hyperboreus*	n/d	Astthorsson and Gislason 1997*
Atlantic cod, *Gadus morhua*	Mixed	*Pandalus borealis, Mallotus villosus*	~60	Jaworski and Ragnarsson 2006*
Haddock, *Melanogrammus aeglefinus*	Mixed	Polychaeta, *Mallotus villosus*, Ophiuroidea	~60	Jaworski and Ragnarsson 2006*
Saithe, *Pollachius virens*	Mixed	*Mallotus villosus*, Ammodytidae, Euphausiacea	~50	Jaworski and Ragnarsson 2006*
Tusk, *Brosme brosme*	Mixed	*Micromesistius poutassou, Munida* sp.	49–62	Bergstad 1991
Ling, *Molva molva*	Mixed	*Gadus morhua, Pollachius virens, Todarodes sagittatus*	60–155	Bergstad 1991
Blue ling, *Molva dypteryia*	Mixed	*Micromesistius poutassou, Argentina silus*, Decapoda	70–79	Bergstad 1991
Atlantic wolffish, *Anarhichas lupus*	Benthic	Echinodermata, Mollusca	~50	Jaworski and Ragnarsson 2006*
European plaice, *Pleuronectes platessa*	Benthic	Polychaeta, Harpacticoida, Amphipoda	~40	Russo et al. 2008
Lemon sole, *Microstomus kitt*	Benthic	Polychaeta, Ophiuroidea, Mollusca	31–40	Steinarsson, 1979*
Redfish (inshore), *Sebastes marinus*	Mixed	*Meganyctiphanes norvegica, Mallotus villosus*	~40	Jaworski and Ragnarsson 2006*
Redfish (offshore), *S. marinus* and *S. mentella*[a]	Pelagic	*Meganyctiphanes norvegica*	31–33	Petursdottir et al. 2008*
Glacial eelpout, *Lycodes frigidus*	Pelagic	*Hymenodora glacialis, Gonatus steenstrupi, Clupea harengus*, Polychaeta, Decapoda	>30	A. Monge and J. Svavarsson, unpublished data*[b]; Bjelland et al. 2000

Note: Only the most frequently observed diet items are provided for each species (i.e., not an exhaustive list). Studies that reported data for fishes sampled from Icelandic waters are marked with an asterisk (*). Size (cm) is the size of the fish for which diet data are provided, and "n/d" indicates that no size data were provided.

[a]Previous diet data provided is for *Sebastes mentella*.

[b]A. Monge and J. Svavarsson, Institute of Biology, University of Iceland, Sturlugata 7, IS-101 Reykjavik, Iceland.

feed primarily on planktonic (Scott and Scott 1988) and benthic invertebrates (Russo et al. 2008), respectively, and the TP of both species was estimated at 3.2.

Previously reported stomach content data for all teleosts sampled were compiled from the literature for comparison to the resource use and TPs indicated by $\delta^{13}C$ and $\delta^{15}N$ in the present study, respectively (Table 3). When possible, data provided in Table 3 were from studies conducted in Icelandic waters and for teleosts of a similar size to the present study's samples.

In an attempt to further differentiate potential energy sources to Greenland sharks, log[Hg] was compared among the four teleost resource use categories (outlined above) using 95% CIs and a subsequent analysis of variance (ANOVA). Simple linear regressions were used to test for relationships between log[Hg] and length for each species separately and for log[Hg] and $\delta^{15}N$ among species. An additive model was then used to investigate the simultaneous effects of resource use category and $\delta^{15}N$ on log[Hg] among all species, with teleosts coded according to their $\delta^{13}C$-assigned resource use category and Greenland sharks coded into a separate category (because they could not be clearly assigned to one category based on $\delta^{13}C$). Likelihood ratio tests are useful for identifying the difference in fit of a more parameterized model relative to a reduced model (Quinn and Keough 2002) and were therefore used to test

whether the fit of the model including both resource use category and $\delta^{15}N$ was improved relative to the model including only $\delta^{15}N$. Likelihood ratio tests were performed using the "lrtest" function in the statistical package "lmtest" in R (R Development Core Team 2008). The effects of sex on $\delta^{13}C$, $\delta^{15}N$, and Hg could not be determined because too few male sharks were sampled and the sex organs of most teleosts had been removed prior to sampling. All analyses were considered significant if $P < 0.05$ for test statistics and were run in R.

Results

Greenland shark stomach contents and $\Delta^{13}C$ and $\Delta^{15}N$

Redfish (i.e., *Sebastes* spp.) had the highest frequency (54.5% of sharks) and highest numbers (303 individual redfish) and contributed the most by weight (325 kg) to the stomachs of Greenland sharks (Table 2). Other teleosts present in the stomachs of Greenland sharks included those that feed pelagically (e.g., greater argentine), benthically (e.g., wolffish, European plaice), and on both benthic and pelagic resources (e.g., Atlantic cod, tusk) based on previous diet data (for references, see Table 3). Tissue from polar bear and unidentified pinniped and cetacean species were also found in the stomachs of Greenland sharks (Table 2).

All teleosts sampled in the present study were identified

1434

Can. J. Fish. Aquat. Sci. Vol. 67, 2010

in the stomachs of Greenland sharks except for capelin, lemon sole, and glacial eelpout (assuming that blue ling could have been present as "Lotidae (unidentified ling, blue ling, tusk)"; Table 2). The $\Delta^{13}C$ and $\Delta^{15}N$ calculated for Greenland sharks based on dietary proportions (Table 2) were 0.4‰ and 4.0‰, respectively.

$\delta^{13}C$ and $\delta^{15}N$ among species

European plaice, wolffish, and lemon sole had similar and significantly higher $\delta^{13}C$ than all other teleosts based on 95% CIs (Fig. 2) and were assigned to a resource use category referred to as "inshore benthic." Capelin (whole fish), glacial eelpout, offshore redfish, and greater argentine had significantly lower $\delta^{13}C$ than the other teleosts based on 95% CIs and were assigned to the "offshore pelagic" resource use category (Fig. 2). The remaining teleosts had intermediate $\delta^{13}C$ values that fell between the inshore benthic and offshore pelagic teleosts. The teleosts with intermediate $\delta^{13}C$ sampled offshore are referred to as "offshore mixed" (i.e., ling, blue ling, tusk), and those sampled inshore are referred to as "inshore mixed" (i.e., cod, haddock, saithe, inshore redfish). Blue ling could have been grouped into a different resource use category, because they had significantly different $\delta^{13}C$ from both the offshore pelagic and offshore mixed fishes. However, because of their close taxonomic relationship with ling and tusk, blue ling was assigned to the offshore mixed resource use category. Several inshore and offshore mixed fishes had similar $\delta^{13}C$ based on 95% CI overlap, despite being sampled at distant locations. For example, the 95% CI of tusk $\delta^{13}C$ overlapped that of Atlantic cod, haddock, saithe, and inshore redfish (Fig. 2), although >200 km separated the sampling locations of tusk and the inshore fishes (Fig. 1).

Values of $\delta^{13}C$ among individual Greenland sharks ranged from –19.7‰ to –15.7‰, with a mean ± 1 standard error (SE) of –17.8‰ ± 0.3‰ (Table 1). The 95% CI of Greenland shark $\delta^{13}C$ overlapped that of teleosts assigned to the offshore pelagic (i.e., greater argentine), offshore mixed (i.e., blue ling, ling), and inshore mixed (i.e., inshore redfish) resource use categories (Fig. 2). Mean Greenland shark $\delta^{13}C$ was closest to that of blue ling (–17.7‰) (Table 1; Fig. 2), but when corrected for by the $\Delta^{13}C$ of 0.4‰ (i.e., subtracted from the mean Greenland shark $\delta^{13}C$ to correct for the enrichment of ^{13}C with TP), it became slightly closer to the $\delta^{13}C$ of the pelagic-feeding greater argentine (Table 1; Fig. 2).

All teleost samples had C–N ratios (C/N) of <3.2, indicating adequate lipid removal (C/N of <3.5 indicates adequate removal of lipid from animal tissues; Post et al. 2007). However, C/N of Greenland shark muscle samples ranged from 3.0 to 4.6, with a mean ± 1 SD of 3.5 ± 0.3. Eleven Greenland sharks had adequate lipid removal (i.e., C/N of <3.5) and the mean ± 1 SD of said sharks' $\delta^{13}C$ was –17.3‰ ± 1.2‰. Therefore, if all lipids had been removed, the mean $\delta^{13}C$ of Greenland sharks would still be most similar to that of mixed-feeding teleosts such as ling and would still be closer to the $\delta^{13}C$ of the pelagic- vs. benthic-feeding teleosts (Table 1; Fig. 2).

Assignment of teleosts to pelagic, mixed, or benthic diets by $\delta^{13}C$ was generally supported by previously reported stomach content data (Table 3). Specifically, the benthic signature of wolffish, lemon sole, and European plaice was

consistent with their consumption of benthic invertebrates (e.g., polychaete worms), and the pelagic signature of capelin, greater argentine, and offshore redfish agreed with their consumption of pelagic zooplankton (Table 3). The pelagic assignment of glacial eelpout agreed with their known consumption of the pelagic shrimp *Hymenodora glacialis* and squid *Gonatus steenstrupi* in Icelandic waters (A. Monge and J. Svavarsson, Institute of Biology, University of Iceland, Sturlugata 7, IS-101 Reykjavik, Iceland, unpublished data), although glacial eelpout from Icelandic waters and the Norwegian Sea are also known to consume benthic prey such as polychaetes (Table 3). The intermediate $\delta^{13}C$ of Atlantic cod, haddock, and saithe is consistent with previous studies that indicated a diet of both benthic (e.g., Ophiuroidea) and pelagic invertebrates (e.g., Euphausiacea) and benthic (e.g., Ammodytidae) and pelagic fishes (e.g., capelin) (Table 3). The assignment of inshore redfish to the mixed resources category in the present study does not agree with previous stomach content data, which indicated pelagic feeding (Table 3). However, redfish (*Sebastes* spp.) from Newfoundland waters were also assigned to mixed feeding (i.e., benthic and pelagic) by $\delta^{13}C$, suggesting that redfish can also consume benthic prey (Sherwood and Rose 2005). The fewest previous diet data existed for the species assigned to the offshore mixed category (i.e., ling, blue ling, and tusk) because of a high frequency of empty stomachs. For example, out of 129 individual tusk (*Brosme brosme*) caught in the North Sea, only four stomachs contained prey (Bergstad 1991). Although based on few data, diet items of ling, blue ling, and tusk from the North Sea included benthic prey such as lobsters (i.e., *Munida* spp.) and pelagic fish (e.g., *Argentina silus*) and squid (e.g., *Todarodes sagittatus*), which supports their designation as mixed feeders by $\delta^{13}C$ (Table 3).

Greenland shark and glacial eelpout had significantly higher $\delta^{15}N$ than all species sampled based on 95% CIs (Table 2; Fig. 2). Regarding relative TPs calculated from $\delta^{15}N$ values, Greenland sharks had the highest calculated TP (4.3) of any species sampled (Table 1). Among teleosts, capelin had the lowest relative TP (3.0), and blue ling and tusk had the highest (3.8) (Table 1). The range of relative TPs among teleosts in the present study was consistent with their known consumption of pelagic zooplankton (e.g., capelin, TP = 3.0), benthic invertebrates (e.g., wolffish, TP = 3.1), or both invertebrates and fish (e.g., cod, TP = 3.7), as indicated by previous stomach content data (Table 3). Regarding the baseline species, $\delta^{15}N$ was significantly higher in deepwater shrimp (baseline for glacial eelpout) than in European plaice (baseline for inshore species) and greater argentine (baseline for offshore species) and did not differ between inshore and offshore baseline species based on 95% CIs (Fig. 2).

Mercury concentrations among species

Capelin and deepwater shrimp did not have detectable levels of Hg (total Hg, µg·g dw^{-1}) (Table 1). Log[Hg] was significantly higher in Greenland sharks relative to all other species sampled based on 95% CIs and generally differed among teleosts assigned to different resource use categories (Fig. 3). Specifically, several inshore mixed fishes (Atlantic cod, haddock, saithe) had significantly lower log[Hg] than all offshore mixed teleosts (ling, blue ling, tusk) and two

offshore pelagic teleosts (glacial eelpout, offshore redfish) based on 95% CIs (Fig. 3). A subsequent ANOVA supported the results from 95% CIs and indicated that resource use category had a significant effect on log[Hg] ($F_{[3,60]}$ = 27.23, P < 0.001), with significant differences in log[Hg] concentrations based on post-hoc comparisons as follows: offshore mixed > offshore pelagic > inshore mixed = inshore benthic. Log[Hg] was not related to length in any species based on linear regressions (all P > 0.05). Among species, log[Hg] significantly increased with δ^{15}N ($y = 0.26x - 3.51$, R^2 = 0.671, P < 0.001). The additive model including both resource use category and δ^{15}N as independent variables indicated that log[Hg] differed with resource use category and that, across categories, log[Hg] significantly increased with δ^{15}N (R^2 = 0.850, P < 0.001). Based on likelihood ratio tests, the model including both resource use and δ^{15}N as predictors of log[Hg] was a better fit than the model including only δ^{15}N (χ^2_4 = 64.19, P < 0.001).

Discussion

Resource use among Greenland sharks and teleosts

The similar δ^{13}C between Greenland sharks and offshore pelagic and mixed teleosts (based on 95% CI overlap) indicates that Greenland sharks in Icelandic waters used both benthic and pelagic resources. Stomachs of Greenland sharks sampled in this study and of Greenland sharks sampled in West Greenland waters (Yano et al. 2007) confirm that Greenland sharks consume benthic (e.g., Atlantic wolffish, *A. lupus*) and pelagic (e.g., redfish, *S. mentella* and *S. marinus*) prey. The similarity between the Δ^{13}C-corrected mean value of Greenland sharks and the mean δ^{13}C of pelagic-feeding greater argentine could indicate a higher input of pelagic carbon to at least some individual Greenland sharks. A previous study in Cumberland Sound, Baffin Island, Canada, also reported significantly lower (i.e., more pelagic) δ^{13}C signatures in Greenland sharks relative to pelagic-feeding ringed (*Pusa hispida*) and harp (*Phoca groenlandica*) seals (Fisk et al. 2002). Additionally, acoustic tags placed on Greenland sharks living under landfast sea ice in the Canadian Arctic (Skomal and Benz 2004) and acoustic and satellite tags placed on Greenland sharks living in the St. Lawrence estuary, Canada (Stokesbury et al. 2005), indicated that Greenland sharks physically visit pelagic environments. Results from δ^{13}C in the present study provided further evidence that pelagic resources are important to at least some Greenland sharks. However, high variability in δ^{13}C among individual Greenland sharks warrants further study (see Bolnick et al. 2003).

The Δ^{13}C of 0.4‰ calculated for Greenland sharks was within the expected increase of 0‰–1‰ frequently reported between an animal and its diet (Fry and Sherr 1984), but was lower than the mean Δ^{13}C value of 0.9‰ ± 0.3‰ (mean ± 1 SD) reported for three captive tiger sharks (*Carcharias taurus*) and one captive lemon shark (*Negaprion brevirostris*) fed a known diet (Hussey et al. 2009). However, isotope discrimination values are currently thought to be diet- and taxa-dependent (Overmyer et al. 2008; Caut et al. 2009; Hussey et al. 2009), and calculating a species-specific discrimination value seemed more appropriate than using a value from the literature.

The agreement between teleost resource use, as indicated by δ^{13}C in the present study, and previously published diet data suggests that δ^{13}C accurately assigned most teleosts to reliance on pelagic, benthic, or mixed resources. The similar δ^{13}C of inshore mixed and offshore mixed teleosts could reflect their feeding on similar prey species or their feeding on different prey with similar δ^{13}C values. The sampling of offshore species in deeper water and ~200 km away from inshore species suggests the latter explanation, although some species (e.g., Atlantic cod; Sherwood and Rose 2005) are likely capable of moving between offshore and inshore habitats. However, because of overlapping δ^{13}C among several mixed species and the lack of stomach content data in the present study, drawing more specific conclusions regarding the diet of mixed teleosts based solely on δ^{13}C values is impossible.

Trophic positions among Greenland sharks and teleosts

Greenland sharks sampled in Icelandic waters had a higher calculated TP relative to known teleost prey. Contrary to this result, Fisk et al. (2002) reported lower than expected δ^{15}N values of Greenland sharks sampled off the coast of Baffin Island, based on similar δ^{15}N among Greenland sharks and two prey species: ringed seal and turbot (*Reinhardtius hippoglossoides*). Fisk et al. (2002) suggested that urea present in Greenland shark tissues (shark liver was analyzed) could have contributed to low observed δ^{15}N. However, urea was recently reported to have no effect on muscle δ^{15}N of spiny dogfish (*Squalus acanthias*) (Logan and Lutcavage 2010). Thus, it is unlikely that urea influenced Greenland shark muscle δ^{15}N values or their calculated TP in the present study.

The Greenland shark specific Δ^{15}N of 4.0‰ was within the published range of isotope discrimination factors previously published for fishes (Vander Zanden and Rasmussen 2001; Caut et al. 2009). However, a Δ^{15}N of 2.3‰ ± 0.2‰ (mean ± 1 SD) was recently reported for captive tiger and lemon sharks, indicating that sharks might have lower Δ^{15}N than teleosts (Hussey et al. 2009). If this is the case, then the Δ^{15}N calculated for Greenland sharks in the present study could be too high (and therefore their TP could be too low). The small number of shark stomachs quantified (n = 22) and the lack of certain prey included in the analysis (e.g., marine mammal) are limitations to the Greenland shark specific Δ^{15}N. Although marine mammals were not sampled in the present study, previous studies have reported similar δ^{15}N values between piscivorous marine mammals and teleosts. For example, muscle of ringed seal and turbot sampled off the coast of Baffin Island had similar δ^{15}N values (Fisk et al. 2002). Therefore, the δ^{15}N of pinnipeds and cetaceans in Icelandic waters is expected to be similar to that of piscivorous teleosts such as Atlantic cod and ling. The lack of marine mammals in the present study is therefore not thought to severely bias the Δ^{15}N calculated for Greenland sharks. Further, as was the case with Δ^{13}C (discussed above), calculating a specific Δ^{15}N for Greenland sharks in the present study seemed more appropriate than using a value from the literature.

The agreement between relative TPs calculated for Icelandic teleosts and previous diet data indicates that TPs were likely accurate and that European plaice, greater argentine,

and deepwater shrimp were appropriate baselines for the inshore and offshore teleosts and glacial eelpout, respectively. Higher $\delta^{15}N$ in deepwater shrimp relative to the other baseline species suggests that baseline $\delta^{15}N$ varied spatially between the deepwater habitat of glacial eelpout and the other sampling areas. This conclusion is supported by the observation that $\delta^{15}N$ varies with depth in the North Atlantic (Velinsky and Fogel 1999). Spatial variability in $\delta^{15}N$ was not apparent between inshore and offshore habitats based on similar $\delta^{15}N$ values (i.e., 95% CI overlap) in European plaice and greater argentine. In Newfoundland waters, however, conspecifics sampled offshore had generally lower $\delta^{15}N$ than those sampled inshore (Sherwood and Rose 2005). Thus, broad-scale patterns of spatial variability in baseline $\delta^{15}N$ (i.e., over a distance of several hundred kilometres) could be ecosystem-specific. The apparent lack of spatial variability in $\delta^{15}N$ between inshore and offshore habitats and the agreement between calculated TP and previous diet data indicate that $\delta^{15}N$ was a good proxy for TP among Iceland species.

Mercury as an additional tracer of diet and resource use

The application of Hg in the present study relied on the assumption that Hg differed among species based on diet and resource use. This assumption appeared valid because log[Hg] was significantly higher in offshore mixed- and pelagic-feeding fishes relative to inshore mixed- and benthic-feeding fishes based on 95% CIs and ANOVA. Log[Hg] also increased with TP (as indicated by $\delta^{15}N$) based on linear regression and was better described by the combination of $\delta^{13}C$-assigned resource use category and $\delta^{15}N$ vs. $\delta^{15}N$ alone, based on a likelihood ratio test. Thus, results from the present study support results from previous studies that both $\delta^{15}N$ and benthic vs. pelagic resource use are important for describing Hg concentrations in fishes (Power et al. 2002; Eagles-Smith et al. 2008).

Significantly higher log[Hg] in offshore mixed- and pelagic-feeding teleosts relative to inshore mixed- and benthic-feeding teleosts could indicate that the high Hg concentrations in Greenland sharks are at least partially explained by their feeding on offshore resources. Similar $\delta^{13}C$ between Greenland sharks and offshore mixed- and pelagic-feeding teleosts supports this suggestion. Of course, teleosts are not the only prey of Greenland sharks based on stomach content data (this study; Fisk et al. 2002), and additional prey such as marine mammals likely contributed to observed Hg concentrations in Greenland sharks. Regardless, the significant difference in log[Hg] between offshore mixed-feeding and inshore mixed-feeding teleosts provided an additional way to separate these species regarding their potential importance to the diet of Greenland sharks. Results from the present study support previous observations that Hg can differ among marine fishes when $\delta^{13}C$ and (or) $\delta^{15}N$ overlap (Bank et al. 2007; Cai et al. 2007).

The significant increase in log[Hg] with $\delta^{15}N$ suggests that TP is an important determinant of Hg concentrations in Icelandic fishes. Additionally, the higher Hg concentrations in Greenland sharks relative to their known teleost prey supports their high relative TP calculated from $\delta^{15}N$ values. The increase in Hg concentration with increasing TP of fishes is well known (e.g., Chumchal and Hambright 2009), and $\delta^{15}N$

has frequently been used to describe Hg variability in aquatic food webs (Cabana and Rasmussen 1994; Kidd et al. 1995; Campbell et al. 2005). Previous studies in marine and freshwater systems have reported a slope of ~0.2 for the relationship between log[Hg] and $\delta^{15}N$ (reviewed by Rigét et al. 2007), which is similar to the slope of 0.26 observed in the present study. Therefore, results from Icelandic fishes support the suggestion by previous researchers (Kidd et al. 2003; Chen et al. 2008; Chumchal and Hambright 2009) that a similar mechanism appears to govern the increase of Hg with TP (i.e., biomagnification) among disparate systems.

Some of the unexplained variability in the log[Hg]–$\delta^{15}N$ linear regression can be explained by differences in Hg concentrations among habitats and (or) resource use, based on the improved fit of the model including both resource use category and $\delta^{15}N$. Although sufficient data did not exist to further investigate trends of Hg accumulation within each resource use category, the mechanism driving generally higher log[Hg] in the offshore mixed- and pelagic-feeding teleosts vs. inshore mixed- and benthic-feeding teleosts could be (i) offshore fishes feeding at a higher TP (Cai et al. 2007), (ii) variability in the uptake and (or) availability of Hg between the bases of the benthic and pelagic food chains (Kidd et al. 2003), or (iii) lower growth rates or higher activity costs in offshore fishes (Trudel and Rasmussen 2006). Feeding at different TPs is a likely explanation for some of the variability in Hg between inshore and offshore species, because the teleosts with the highest relative TPs were those sampled offshore (i.e., tusk and blue ling, TPs = 3.8). The influence of Hg variability between the base of benthic and pelagic food chains and the potential influence of growth rate and activity cost on fish Hg cannot be assessed in the present study. However, results from Icelandic fishes suggest that Hg varies with TP and resource use and stress the need for additional data concerning log[Hg] bioaccumulation between benthic and pelagic food chains in marine environments (Chen et al. 2008).

High Hg in Greenland sharks sampled in the present study was attributed to their feeding at a high TP and on slightly more contaminated offshore resources, although the bioaccumulation of Hg in tissues over time can also contribute to observed Hg concentrations in fish (Trudel and Rasmussen 2006). It is currently impossible to age Greenland sharks, but if Hg accumulation over time (i.e., age) was an important mechanism governing observed Greenland shark Hg concentrations, a positive increase in log[Hg] with shark length would be expected. The lack of a relationship between Greenland shark length and log[Hg] indicates that (i) Hg in larger, assumedly older Greenland sharks was not entirely driven by bioaccumulation over time and (ii) the larger Greenland sharks sampled in the present study did not necessarily feed at a higher TP than smaller sharks. Greenland sharks ranging from 234 to 322 cm (fork length) sampled in Cumberland Sound, Baffin Island, Canada, also did not exhibit a relationship between hepatic log[Hg] and length (McMeans et al. 2007). The lack of a relationship between length and log[Hg] within Icelandic teleosts could be attributed to the small size range and (or) low number of each species sampled, because many fishes are known to ex-

hibit increased Hg concentrations with size and age (e.g., Eagles-Smith et al. 2008).

Temporal variability in $\delta^{13}C$, $\delta^{15}N$ (Nordström et al. 2009), and Hg (Lambertsson and Nilsson 2006) could also have influenced the interpretation of Greenland shark diet in the present study. The sampling of Greenland sharks opportunistically as bycatch prevented their collection during a smaller time frame. Although it is impossible to identify if temporal variability influenced results in the present study, sampling year (categorical variable) did not significantly reduce the unexplained variability in $\delta^{13}C$ (ANOVA, $F_{[4,14]}$ = 0.998, $P > 0.05$), $\delta^{15}N$ ($F_{[4,14]} = 2.659$, $P > 0.05$), or log[Hg] ($F_{[4,13]} = 0.375$, $P > 0.05$) among individual Greenland sharks. Temporal variability was likely not an issue for Icelandic teleosts because they were all collected during a four-month period (i.e., between August and November 2005), except for capelin and glacial eelpout. The agreement between previous diet data and this study's assigned resource use (indicated by $\delta^{13}C$) and TPs (indicated by $\delta^{15}N$) supports this suggestion.

Acknowledgements

References

Astthorsson, O.S., and Gislason, A. 1997. On the food of capelin in the subarctic waters north of Iceland. Sarsia, **82**(2): 81–86.

Bank, M.S., Chesney, E., Shine, J.P., Maage, A., and Senn, D.B. 2007. Mercury bioaccumulation and trophic transfer in sympatric snapper species from the Gulf of Mexico. Ecol. Appl. **17**(7): 2100–2110. doi:10.1890/06-1422.1. PMID:17974344.

Becker, D.S., and Bigham, G.N. 1995. Distribution of mercury in the aquatic food-web of Onondaga Lake, New York. Water Air Soil Pollut. **80**(1–4): 563–571. doi:10.1007/BF01189706.

Bergstad, O.A. 1991. Distribution and trophic ecology of some gadoid fish of the Norwegian deep. 1. Accounts of individual species. Sarsia, **75**(4): 269–313.

Bjelland, O., Bergstad, O.A., Skjæraasen, J.E., and Meland, K. 2000. Trophic ecology of deep-water fishes associated with the continental slope of the eastern Norwegian Sea. Sarsia, **85**: 101–117.

Bligh, E.G., and Dyer, W.J. 1959. A rapid method of total lipid extraction and purification. Can. J. Physiol. Pharmacol. **37**: 911–917. doi:10.1139/y59-099.

Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., and Forister, M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. Am. Nat. **161**(1): 1–28. doi:10.1086/343878. PMID: 12650459.

Cabana, G., and Rasmussen, J.B. 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature (London), **372**(6503): 255–257. doi:10.1038/372255a0.

Cai, Y., Rooker, J.R., Gill, G.A., and Turner, J.P. 2007. Bioaccumulation of mercury in pelagic fishes from the northern Gulf of Mexico. Can. J. Fish. Aquat. Sci. **64**(3): 458–469. doi:10.1139/F07-017.

Campbell, L.M., Norstrom, R.J., Hobson, K.A., Muir, D.C.G., Backus, S., and Fisk, A.T. 2005. Mercury and other trace elements in a pelagic Arctic marine food web (Northwater Polynya, Baffin Bay). Sci. Total Environ. **351–352**: 247–263. doi:10.1016/j.scitotenv.2005.02.043. PMID:16061271.

Caut, S., Angulo, E., and Courchamp, F. 2009. Variation in discrimination factors ($\Delta^{15}N$ and $\Delta^{13}C$): the effect of diet isotopic values and applications for diet reconstruction. J. Appl. Ecol. **46**(2): 443–453. doi:10.1111/j.1365-2664.2009.01620.x.

Chen, C., Amirbahman, A., Fisher, N., Harding, G., Lamborg, C., Nacci, D., and Taylor, D. 2008. Methylmercury in marine ecosystems: spatial patterns and processes of production, bioaccumulation, and biomagnification. EcoHealth, **5**(4): 399–408. doi:10.1007/s10393-008-0201-1. PMID:19015919.

Chumchal, M.M., and Hambright, K.D. 2009. Ecological factors regulating mercury contamination of fish from Caddo Lake, Texas, U.S.A. Environ. Toxicol. Chem. **28**(5): 962–972. doi:10.1897/08-197.1. PMID:19049260.

Chumchal, M.M., Drenner, R.W., Fry, B., Hambright, K.D., and Newland, L.W. 2008. Habitat-specific differences in mercury concentration in a top predator from a shallow lake. Trans. Am. Fish. Soc. **137**(1): 195–208. doi:10.1577/T07-009.1.

Davenport, S.R., and Bax, N.J. 2002. A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Can. J. Fish. Aquat. Sci. **59**(3): 514–530. doi:10.1139/f02-031.

Eagles-Smith, C.A., Suchanek, T.H., Colwell, A.E., and Anderson, N.L. 2008. Mercury trophic transfer in a eutrophic lake: the importance of habitat-specific foraging. Ecol. Appl. **18**(8, Suppl.): A196–A212. doi:10.1890/06-1476.1.

Fisk, A.T., Tittlemier, S.A., Pranschke, J.L., and Norstrom, R.J. 2002. Using anthropogenic contaminants and stable isotopes to assess the feeding ecology of Greenland sharks. Ecology, **83**(8): 2162–2172. doi:10.1890/0012-9658(2002)083[2162:UACASI]2.0.CO;2.

Fry, B., and Sherr, E.B. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci. **27**: 13–47.

Harris, R.C., and Bodaly, R.A. 1998. Temperature, growth and dietary effects on fish mercury dynamics in two Ontario lakes. Biogeochemistry, **40**(2–3): 175–187. doi:10.1023/A:1005986505407.

Hussey, N.E., Brush, J., McCarthy, I.D., and Fisk, A.T. 2009. ^{15}N and ^{13}C diet–tissue discrimination factors for large sharks under semi-controlled conditions. Comp. Biochem. Physiol. A, **155**(4): 445–453. doi:10.1016/j.cbpa.2009.09.023.

Jaworski, A., and Ragnarsson, S.A. 2006. Feeding habits of demersal fish in Icelandic waters: a multivariate approach. ICES J. Mar. Sci. **63**(9): 1682–1694. doi:10.1016/j.icesjms.2006.07.003.

Kidd, K.A., Hesslein, R.H., Fudge, R.J.P., and Hallard, K.A. 1995. The influence of trophic level as measured by $\delta^{15}N$ on mercury concentrations in freshwater organisms. Water Air Soil Pollut. **80**(1–4): 1011–1015. doi:10.1007/BF01189756.

Kidd, K.A., Bootsma, H.A., Hesslein, R.H., Lockhart, L., and Hecky, R.E. 2003. Mercury concentrations in the food web of Lake Malawi, East Africa. J. Great Lakes Res. **29**(2): 258–266. doi:10.1016/S0380-1330(03)70553-X.

Lambertsson, L., and Nilsson, M. 2006. Organic material: the primary control on mercury methylation and ambient methyl mercury concentrations in estuarine sediments. Environ. Sci.

1438

Can. J. Fish. Aquat. Sci. Vol. 67, 2010

Technol. **40**(6): 1822–1829. doi:10.1021/es051785h. PMID: 16570603.

Logan, J.M., and Lutcavage, M.E. 2010. Stable isotope dynamics in elasmobranch fishes. Hydrobiologia, **644**(1): 231–244. doi:10.1007/s10750-010-0120-3.

McMeans, B.C., Borgå, K., Bechtol, W.R., Higginbotham, D., and Fisk, A.T. 2007. Essential and non-essential element concentrations in two sleeper shark species collected in arctic waters. Environ. Pollut. **148**(1): 281–290. doi:10.1016/j.envpol.2006.10.039. PMID:17182159.

Nordström, M., Aarnio, K., and Bonsdorff, E. 2009. Temporal variability of a benthic food web: patterns and processes in a low-diversity system. Mar. Ecol. Prog. Ser. **378**: 13–26. doi:10.3354/meps07872.

Overmyer, J.P., Macneil, M.A., and Fisk, A.T. 2008. Fractionation and metabolic turnover of carbon and nitrogen stable isotopes in black fly larvae. Rapid Commun. Mass Spectrom. **22**(5): 694–700. doi:10.1002/rcm.3413. PMID:18257111.

Payton, M.E., Greenstone, M.H., and Schenker, N. 2003. Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? J. Insect Sci. **3**: 34–40. PMID:15841249.

Petursdottir, H., Gislason, A., Falk-Petersen, S., Hop, H., and Svavarsson, J. 2008. Trophic interactions of the pelagic ecosystem over the Reykjanes Ridge as evaluated by fatty acid and stable isotope analyses. Deep Sea Res. II Top. Stud. Oceanogr. **55**(1–2): 83–93. doi:10.1016/j.dsr2.2007.09.003.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, **83**(3): 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montaña, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia (Berl.), **152**(1): 179–189. doi:10.1007/s00442-006-0630-x.

Power, M., Klein, G.M., Guiguer, K., and Kwan, M.K.H. 2002. Mercury accumulation in the fish community of a sub-Arctic lake in relation to trophic position and carbon sources. J. Appl. Ecol. **39**(5): 819–830. doi:10.1046/j.1365-2664.2002.00758.x.

Quinn, G.P., and Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/.

Rigét, F., Møller, P., Dietz, R., Nielsen, T.G., Asmund, G., Strand, J., Larsen, M.M., and Hobson, K.A. 2007. Transfer of mercury in the marine food web of West Greenland. J. Environ. Monit. **9**(8): 877–883. doi:10.1039/b704796g. PMID:17671670.

Russo, T., Pulcini, D., O'Leary, A., Cataudella, S., and Mariani, S. 2008. Relationship between body shape and trophic niche segregation in two closely related sympatric fishes. J. Fish Biol. **73**(4): 809–828. doi:10.1111/j.1095-8649.2008.01964.x.

Sarà, G., De Pirro, M., Sprovieri, M., Rumolo, P., Halldórsson, H.P., and Svavarsson, J. 2009. Carbon and nitrogen stable isotopic inventory of the most abundant demersal fish captured by benthic gears in southwestern Iceland (North Atlantic). Helgol. Mar. Res. **63**(4): 309–315. doi:10.1007/s10152-009-0159-6.

Scott, W.B., and Scott, M.G. 1988. Atlantic fishes of Canada. University of Toronto Press, Toronto, Ontario, Canada.

Sherwood, G.D., and Rose, G.A. 2005. Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf food web. Estuar. Coast. Shelf Sci. **63**(4): 537–549. doi:10.1016/j.ecss.2004.12.010.

Skomal, G.B., and Benz, G.W. 2004. Ultrasonic tracking of Greenland sharks, *Somniosus microcephalus*, under Arctic ice. Mar. Biol. (Berl.), **145**(3): 489–498. doi:10.1007/s00227-004-1332-8.

Steinarsson, B. 1979. Food of lemon sole (*Microstomus kitt* Walbaum), Megrim (*Lepidorhombus whiffiagonis* Walbaum) and Witch (*Glyptocephalus cynoglossus* L) in Icelandic waters. Meeresforschung Rep. Mar. Res. **27**(3): 156–171.

Stokesbury, M.J.W., Harvey-Clark, C., Gallant, J., Block, B.A., and Myers, R.A. 2005. Movement and environmental preferences of Greenland sharks (*Somniosus microcephalus*) electronically tagged in the St. Lawrence Estuary, Canada. Mar. Biol. (Berl.), **148**(1): 159–165. doi:10.1007/s00227-005-0061-y.

Trudel, M., and Rasmussen, J.B. 2006. Bioenergetics and mercury dynamics in fish: a modelling perspective. Can. J. Fish. Aquat. Sci. **63**(8): 1890–1902. doi:10.1139/F06-081.

Vander Zanden, M.J., and Rasmussen, J.B. 1999. Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. Ecology, **80**(4): 1395–1404. doi:10.1890/0012-9658(1999)080[1395:PCCANA]2.0.CO;2.

Vander Zanden, M.J., and Rasmussen, J.B. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. **46**(8): 2061–2066.

Velinsky, D.J., and Fogel, M.L. 1999. Cycling of dissolved and particulate nitrogen and carbon in the Framvaren Fjord, Norway: stable isotopic variations. Mar. Chem. **67**(3–4): 161–180. doi:10.1016/S0304-4203(99)00057-2.

Yano, K., Stevens, J.D., and Compagno, L.J.V. 2007. Distribution, reproduction and feeding of the Greenland shark *Somniosus* (*Somniosus*) *microcephalus*, with notes on two other sleeper sharks, *Somniosus* (*Somniosus*) *pacificus* and *Somniosus* (*Somniosus*) *antarcticus*. J. Fish Biol. **70**(2): 374–390. doi:10.1111/j.1095-8649.2007.01308.x.