Science of the Total Environment 631–632 (2018) 233–238

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Ecotoxicoparasitology of the gastrointestinal tracts of pinnipeds: the effect of parasites on the potential bioavailability of total mercury (THg)

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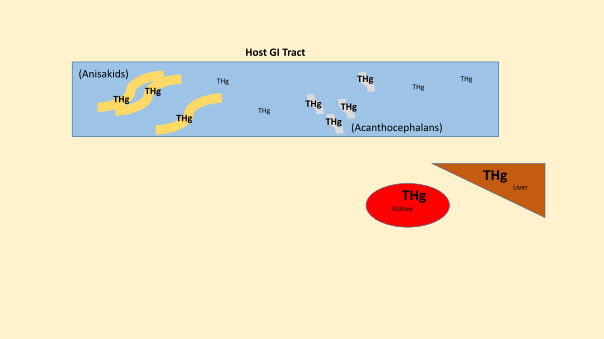
HIGHLIGHTS

- [THg] in the GI tract and parasites was determined for seals and sea lions.
- The goal was to determine the toxicant-parasite relationships within the GI tract.
- [THg] and stable isotopes provide insight on host-parasite-Hg interactions.
- [THg] varies within the GI tract and may be influenced by the presence of parasites.
- [THg] are highest in acanthocephalans compared to other parasitic groups.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 14 December 2017
Received in revised form 8 February 2018
Accepted 14 February 2018
Available online xxxx

Editor: Mae Mae Sexauer Gustin

Keywords:
Stable isotope
Corynosoma
Cestode
Nematode
Anisakid
Acanthocephalan

ABSTRACT

Acanthocephalans, cestodes, and some species of nematodes acquire nutrients from the lumen contents in the gastrointestinal (GI) tract of their definitive host. These parasites are exposed to toxicants, such as mercury (Hg), through passive or active feeding mechanisms; therefore, the focus of this study was to determine if there is an effect of parasites on the dietary availability of total mercury (THg) within piscivorous pinniped hosts. THg concentrations ([THg]) in selected host tissues, parasites, and GI lumen contents from 22 California sea lions (*Zalophus californianus*), 15 ringed seals (*Phoca hispida*), and 4 spotted seals (*Phoca largha*) were determined. Among all pinnipeds, [THg] in acanthocephalans of the large intestine were significantly higher than concentrations in other samples (host lumen contents, other parasites and host intestinal wall), irrespective of location within the host GI tract. $\delta^{15}N$ values of parasites depended both on parasite group and location within the GI tract. $\delta^{15}N$ values were consistently higher in parasites inhabiting the large intestine, compared to elsewhere in the GI tract, for both sea lions and seals. $\delta^{13}C$ values in parasites did not differ significantly from host GI tissues. Based on both [THg] and stable isotope values, parasites are likely affecting the Hg bioavailability within the GI lumen contents and host tissues, and toxicant-parasite interactions appear to depend on both parasitic taxon as well as their location within the host intestine.

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https://doi.org/10.1016/j.scitotenv.2018.02.173
0048-9697/

1. Introduction

Few investigations have explored the ecotoxicoparasitology of marine systems, the study of the relationships among host organisms, their parasite populations, and the toxicants to which both are exposed (McGrew et al. 2015). Effective approaches exist for studying these relationships, and well established tools such as stable isotope analysis and the measurement of toxicant distributions in host-parasite systems, can contribute to a better understanding of feeding ecology, food web structure, and contaminant transfer (Campbell et al. 2005; Finger et al. 2017; McGrew et al. 2015; McHuron et al. 2016).

Mercury (Hg) is a ubiquitous, non-essential element. Natural sources (e.g. volcanic activity, forest fires, natural weathering of rocks), as well as anthropogenic sources, contribute Hg to the environment and associated biota. Mercury is subject to long-range transport by winds and ocean currents, and its occurrence in marine food webs has been, in part, attributed to anthropogenic sources from distant regions (Muir et al. 1999). Consumer exposure to Hg in marine systems is of concern because of the widespread nature of this contaminant, its ability to biomagnify in food webs, and the potential for long range atmospheric transport (Alava et al. 2017; AMAP 2011). Hg has a wide spectrum of effects on health, depending upon the chemical forms and modes of exposure (Hansen and Gilman 2005; Satoh 2003), and increased exposure can have important implications on human and wildlife populations (Van Hoomissen et al., 2017; Rea et al. 2013; Sonne et al., 2009). Monomethylmercury ($MeHg^{+}$), produced by microbial methylation of inorganic Hg, becomes integrated into the food web at lower trophic levels, and is then subject to biomagnification in higher trophic-level organisms such as fish (Kruzikova et al., 2008) and marine mammals (Dehn et al. 2006; McHuron et al. 2014). As top predators in marine food webs, piscivorous marine mammals generally have elevated total mercury concentrations ([THg]) in their tissues (Braune et al. 2005; McHuron et al. 2014; Moses et al., 2009).

It is well established that parasites play an important role in food webs (Lafferty et al. 2008), but host-parasite interactions, in the context of contaminants, have received far less attention. Often, parasites are transmitted trophically to their host through their food source. Many helminths, including nematodes, cestodes, and acanthocephalans, that live in the gastrointestinal (GI) tracts of their definitive hosts, feed on GI lumen contents through passive or active mechanisms as nutrients from the host lumen contents are ingested or taken up across parasite's tegument. These organisms are also exposed to toxicants (i.e. Total Hg (THg)) present in lumen contents. Intestinal helminths occupy distinct niches within the host GI tract, and are known to compete for host nutrients in instances of co-infection (Holmes 1961). They can also alter resource availability and trophic niche of their hosts (Britton and Andreou 2016); conversely, host diet can alter or influence the specific composition of parasite communities (Friesen and Roth, 2016).

Some toxicants have been shown to bioaccumulate in parasites at concentrations orders of magnitude higher than host tissues (Sures et al. 1999). The accumulation of non-essential elements in the parasites of marine organisms has been studied (Courtney-Hogue 2016; Monteiro et al. 2016; Van Hees and Ebert, 2017). Separately, associations between [THg] and stable N isotopes in marine mammals have been explored (Brookens et al. 2008; Friesen and Roth 2016), but the relationships among toxicants, stable isotopes and marine mammal parasites have not been investigated to date.

The purpose of this study was to compare [THg] in multiple matrices (i.e. GI tissues, lumen contents, parasites), and to determine the toxicant-parasite relationships within the GI tracts of pinnipeds from two locations: California, USA (California sea lions (*Zalophus californianus*)), and Alaska, USA (ringed seals (*Phoca hispida)* and spotted seals (*Phoca largha*)). While the intent was not to make direct comparisons between these pinniped species, the opportunity to explore ecotoxicoparasitological relationships and Hg exposure in two distinct geographical regions, and among three host species, provided insight into these host-parasite-toxicant systems. In order to better define the ecological relationships between Hg exposure and uptake by parasites and their hosts, we compared [THg] and stable isotope values (C and N) in parasites, GI tissues, and GI lumen contents, based on parasite group, and their location within the host GI tract. Liver and kidney [THg] were used to provide relative estimates of overall host exposure to Hg. Bioaccumulation factors were used to demonstrate whether or not parasites were bioaccumulating THg. We hypothesized that parasites are capable of THg uptake in pinniped hosts, and that [THg] varies based on location within the host GI tract due to complex host-parasite interactions. Interactions between host exposure to THg, host diet, GI parasite community composition, and interspecies competition are factors likely contributing to [THg] within the pinniped host. THg bioaccumulation by parasites may potentially be of benefit to infected host populations with a subsequent decreased bioavailability of THg to the parasitized pinniped.

2. Materials and methods

2.1. Sample collection

Twenty two California sea lions that stranded along the central coast of California, were transported to The Marine Mammal Center (TMMC) (Sausalito, CA) in June 2010. Individuals either stranded dead, died in transport, or were alive upon stranding and underwent rehabilitative efforts at TMMC for up to 15 days, prior to death. They were then necropsied and samples were collected within 48 h of death. This work was conducted under the authorization of NOAA Fisheries. Ice seals were harvested by subsistence hunters in the fall of 2009 (10 ringed seals and 2 spotted seals) and 2010 (5 ringed seals and 2 spotted seals) in Kotzebue Sound, Alaska (USA). Seals were sampled with support provided by the Native Village of Kotzebue under permit No. 932-1905-00IMA-009526 issued by the National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service (USFWS) under the authority of the Marine Mammal Protection Act (MMPA) and Endangered Species Act (ESA).

Sex was determined for each animal, and liver, kidney, and GI tissue samples were collected. During GI processing, stomach, large intestine (LI) and small intestine (SI) were opened longitudinally, using stainless steel instruments, and all macroparasites were manually removed with forceps from the GI tract, sorted by helminth type, and weighed. Nematodes and acanthocephalans were enumerated. Mean intensity and prevalence were determined as defined by Bush et al. (1997). Parasites were frozen at −20 °C for future [THg] determination, and C and N stable isotope analysis. Lumen contents and GI tissue sections (2 × 2 cm, full-thickness) were collected from stomach, proximal and distal small intestine (dSI), and colon. Representative acanthocephalans and nematodes were fixed in 10% buffered formalin, and later identified based on morphological criteria (Anderson et al. 1974; Rausch et al. 2010; Van Cleave 1953).

2.2. Total mercury (THg) analysis

Host samples were thawed at room temperature. Tissues were subsampled (70–150 mg) using stainless steel forceps and scissors. Instruments were washed with ultrapure water and dried between each sample. [THg] is reported on a wet weight (ww) basis as ng/g, but also converted to dry weight (dw) to ensure that observed differences were not driven by variations in moisture content. Parasite [THg] were measured on a dw basis and converted to ww concentrations, as freeze drying the parasites allowed them to be fully homogenized with a mortar and pestle prior to THg and stable isotope analyses. Weights were obtained before and after the freeze-drying process in order to calculate percent moisture. Samples were analyzed on a Milestone DMA-80 instrument (Butala et al. 2006; EPA 600-R-04-012) following procedures

outlined in McHuron et al. (2014). The method detection limit for THg determination was 0.005 ng/g. Quality assurance and quality control (QA/QC) samples included instrument and method blanks, standard reference materials (SRMs), check standards, and sample duplicates. All samples were run in duplicate and re-analyzed if the percent difference was >10%. The SRM utilized was DORM-3 fish protein homogenate (National Resource Council Canada; 0.382 ± 0.060 ng Hg/g). Percent recovery for check standards (5, 20, and 100 ng aqueous Hg) was >90%. Analysis of the standard reference material was within 10% of the certified value for Hg.

2.3. Carbon and nitrogen stable isotope analyses

In preparation for stable isotope analysis, all samples were freeze-dried and ground to a fine powder using a mortar and pestle. Samples were further homogenized using a mini-bead beater (BioSpec). Approximately 1.5 to 2.0 mg of liver and muscle tissue were loaded into separate 5 × 9 mm tin capsules for carbon (C) and nitrogen (N) stable isotope analyses by continuous-flow isotope-ratio mass spectrometry using an elemental analyzer (Carlo Erba NC1500) interfaced to a mass spectrometer (Micromass Optima). Isotope values are reported in delta (δ) notation:

$$\delta X = \left(R_{sample}/R_{standard}\right) \quad (1)$$

where X represents ^{13}C, or ^{15}N in parts per thousand (‰) deviation relative to the reference standard, and R_{sample} and $R_{standard}$ represent the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, for sample and standard, respectively. Isotopic data were normalized to V-PDB and Air, using the primary standards USGS 40 (−26.24‰ and −4.52‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively), USGS 41 (37.76‰ and 47.57‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively). Analytical error was assessed by replicate measures of primary standards (<0.2‰ for both C and N stable isotopes across all analytical sequences) and quality control assessed using several secondary standards analyzed several times within individual analytical sequences (<0.2‰). Accuracy was assessed using primary standards as unknowns, and was within 0.2‰ for both C and N stable isotopes. Sample reproducibility was generally better than 0.2‰.

2.4. Data analyses

Bioaccumulation factors (BAF) were calculated as the ratio of the [THg] in the consumer, relative to the concentration in the food-source (i.e. [THg] within parasite:[THg] within host lumen contents) (McGrew et al. 2015). Therefore, BAFs for this study were determined by dividing the [THg] (ww) in a group of parasites, within a given region of the host GI tract, by the [THg] (ww) in the lumen contents of that same region. [THg] in the SI were obtained by taking the mean [THg] in the proximal and distal small intestine. Ratios of [THg] in intestinal wall compared to lumen contents were also determined for each section of the GI tract, for reference purposes. The BAFs were deemed statistically significant when 95% confidence limits of the means indicated both the upper and lower bounds were >1.0.

Statistical analyses were performed using StatCrunch5.0 statistical software (Integrated Analytics LLC, Pearson Education, 2007–2009). Normality of data was first assessed visually using box plots and frequency distributions. Shapiro-Wilk tests were used, and transformations were carried out; however, data transformations were unable to resolve non-normal distributions and heterogeneity of variance. Non-parametric approaches were determined to be most appropriate for assessment of these data. To determine whether differences existed in [THg] or stable isotope values, based on region of the GI tract or parasitic group, a Kruskal Wallis test was used to determine whether significant differences existed between medians of at least two groups, and then Mann Whitney-*U* tests with Bonferroni-corrected *alpha* values, were used to determine specific differences between pairs. For all tests, $p < 0.05$ was considered significant.

3. Results

3.1. Host information

All spotted seals were female, whereas the ringed seals included 10 females, 4 males, and one individual for which sex was not determined. Among the 22 California sea lions, 14 were male, 7 were female, and there was one individual for which sex was unknown. These California sea lions spent up to 15 days under care at TMMC prior to necropsy, with an average of 6.5 days in rehabilitation. Individuals were predominantly yearlings (n = 19), but also included a juvenile and a two year old.

3.2. Parasite prevalence and distribution

Cestodes were detected exclusively in the SI and nematodes were found in the stomach and SI (Table 1). Acanthocephalans were found in both the SI and LI. Among California sea lions, acanthocephalan species were found in distinct regions of the GI tract. Among infected individuals, 16/20 (80%) harbored *Corynosoma strumosum*, and 100% of these were located in the SI of the host. Nine out of 20 (45%) harbored *C. obtuscens* that was predominantly located in the LI (7/9 individuals). All nematodes belonged to the family Anisakidae.

3.3. [THg] in California sea lions and their parasites

There was no significant difference between [THg] in the stomach wall and gastric nematodes (Table 2); however, both had significantly higher [THg] relative to the stomach contents. In the proximal small intestine (pSI), there was a significant positive association between [THg] of the lumen contents, and concentrations in both acanthocephalans ($p = 0.0436$, corr. coeff = 0.49) and cestodes ($p = 0.0493$, corr. coeff = 0.53). In the LI, mean [THg] in acanthocephalans was significantly higher than in either the LI wall or the colon contents, and mean [THg] in colon contents were significantly higher than concentrations in the LI wall.

Among parasitic groups, LI acanthocephalans had significantly higher [THg] than gastric nematodes, SI acanthocephalans, and SI cestodes (Table 2). [THg] in gastric nematodes were significantly higher than concentrations in SI cestodes, but not significantly higher than in acanthocephalans or nematodes of the SI. Within the SI, [THg] in parasites were related as follows: nematodes = acanthocephalans > cestodes.

Gastric nematodes had a BAF of 3.7 (Fig. 1), and BAF values were significantly higher than 1.0 (95% CL = 1.6 to 5.8). In the SI, BAFs of nematodes, acanthocephalans and cestodes were 1.5, 1.1, and 0.8, respectively. LI acanthocephalans had the highest BAF of 6.7, also significantly higher than 1.0 (95% CL = 2.46 to 10.85). Ratios of [THg] in intestinal wall:[THg] in lumen contents were 1.5, 0.9, and 0.5 for stomach, SI, and LI, respectively.

3.4. [THg] in ice seals and their parasites

There was no significant difference between [THg] in stomach contents, and those in gastric nematodes (Table 2). Likewise, there was no significant difference in [THg] in lumen contents of the pSI or dSI, SI acanthocephalans, or SI nematodes. In the LI, [THg] in the acanthocephalans was significantly higher than concentrations in the intestinal wall; and, as with the California sea lions, [THg] in colon contents was elevated relative to the LI wall. In comparing [THg] among parasitic groups, median concentrations in the LI acanthocephalans were also significantly higher than concentrations observed in SI acanthocephalans.

Table 1
Parasite prevalence and mean intensity (MI) observed in a) California sea lions, and b) ice seals; parasite groups include acanthocephalans (A), cestodes (C), and nematodes (N), and co-infections are shown as combinations of these three groups.

Host or parasite group	Prevalence (%, 95%CI)	Mean intensity (Range)	Acanthocephalan species	Prevalence
a)				
California sea lions				
Acanthocephalans	20/22 (90.9%; 69.4%, 98.4%)	135 (1–909)	*C. strumosum*	16/22 (72.7%)
			C. obtuscens	9/22 (40.9%)
			Both species	5/22 (22.7%)
Cestodes	16/22 (72.7%; 49.6%, 88.4%)	N/A		
Nematodes	20/22 (90.9%; 69.4%, 98.4%)	61 (2–422)		
A + C	14/22 (63.6%; 43.5%, 83.7%)			
A + N	18/22 (81.8%; 65.7%, 97.9%)			
C + N	15/22 (68.2%; 48.7%, 87.6%)			
A + C + N	13/22 (59.1%, 38.5%, 79.6%)			
b)				
Ringed seals				
Acanthocephalans	15/15 (100%; 74.7%, 100%)	90 (2–247)	*C. strumosum*	9/14 (64.3%)
			C. semerme	9/14 (64.3%)
			C. wegeneri	1/14 (7.1%)
Cestodes	1/15 (6.7%; 1.2%, 29.8%)			
Nematodes	7/15 (46.7%; 22.3%, 72.6%)	7 (2–19)		
A + C	0/15 (0%; 0%, 25.3%)			
A + N	7/15 (46.7%; 22.3%, 72.6%)			
C + N	0/15 (0%; 0%, 25.3%)			
A + C + N	1/15 (6.7%; 1.2%, 29.8%)			
Spotted seals				
Acanthocephalans	4/4 (100%; 39.6%, 100%)	874 (362–1818)		
			C. strumosum	1/3 (33.3%)
			C. semerme	2/3 (66.7%)
Cestodes	0/4 (0%; 0%, 60.4%)			
Nematodes	3/4 (75%; 21.9%, 98.7%)	11 (3–17)		
A + C	0/4 (0%; 0%, 60.4%)			
A + N	3/4 (75%; 21.9%, 98.7%)			
C + N	0/4 (0%; 0%, 60.4%)			
A + C + N	0/4 (0%; 0%, 60.4%)			

Similar to California sea lions, BAFs in seal parasites were significantly higher than 1.0 among the LI acanthocephalans, and the mean BAF (2.6, 1.28 to 3.92) was higher than that of any other parasitic group. SI nematodes had a BAF of 0.9 and SI acanthocephalans had a BAF of 1.4. Ratios of [THg] in intestinal wall:lumen contents were determined to be 0.9, 1.2, and 0.5 for stomach, SI, and LI, respectively.

3.5. C and N stable isotopes

In ice seals, nitrogen isotope values in all parasites were lower relative to host GI lumen contents. While most parasites occupy the same trophic level as the host, SI acanthocephalans appear to be feeding approximately one trophic level lower than the host (Table 3). Among all parasites, nitrogen isotope values were highest in gastric nematodes and LI acanthocephalans. $\delta^{13}C$ values in parasites did not differ significantly from host GI tissues.

4. Discussion

The acanthocephalans, cestodes, and nematodes found in both ice seals and sea lions were expected based on host species and geographic location (Margolis, 1955; Margolis and Daily 1972; Van Cleave 1953). These parasites are ubiquitous in their distribution and their presence in marine mammals is common.

Parasites are known to actively select specific sites in their hosts, and may be found in very restricted microhabitats; or, they may move to new areas within the host, as they mature (Holmes 1972). In this study, *Corynosoma strumosum* was the predominant acanthocephalan species found in the SI of the California sea lions, whereas all of the acanthocephalans found in the LI were of the species, *Corynosoma obtuscens*. The latter species clearly had the greatest potential for THg uptake, as demonstrated by the highest BAF values. This supports the likelihood that differences in THg uptake, and a parasite's niche within the host GI tract, may be species specific.

In the California sea lions, mean intensities for both acanthocephalans and nematodes were high, relative to the ice seals. Mean [THg] was also consistently higher in the sea lions. While a link between contaminants and the increased prevalence of infectious disease has been reported in marine mammals (Nakayama et al. 2009), these specific differences may be also be due to the host's trophic position, geographic influences on THg exposure, diet, host immune status, or other factors such as climate.

The presence of parasitic infection has traditionally been thought of as being detrimental to the health of their host; however, more subtle effects of parasitism—both positive and negative—on host populations remain poorly understood. In recent years, parasites have begun to be recognized for their importance in ecosystems, and their ability to affect food web structure, stability and energy flow (Lafferty et al. 2008; Dunne et al., 2013). The combined effects of parasitism and pollution on host health has become a growing area of interest (Sures et al. 2017), and the ability of certain helminth groups to bioaccumulate non-essential elements has been demonstrated in numerous studies (McGrew et al. 2015; Sures 2008; Sures et al. 1999; Courtney-Hogue 2016).

The integral role of parasites in ecosystems may also relate to host-parasite co-evolution, in which case, THg uptake by parasites may be an adaptation of the parasite, rather than simply the result of passive feeding mechanisms. It is possible that parasites may possess

Table 2
Total mercury concentrations (ppb, ww) in tissues and parasites from California sea lions, and ringed seals and spotted seals.

Tissue or parasite	n	Mean	Median	Range
California sea lions				
Liver	20	9259.7	5052.2	1623.4–34,945.5
Kidney	20	1173.1	1070.8	431.9–2436.0
Stomach wall	22	113.0	100.3	55.7–232.3
Stomach contents	18	76.4	43.0	6.5–199.4
Proximal SI wall	21	98.5	96.6	48.6–190.7
Proximal SI lumen	21	89.7	72.8	21.5–211.4
Distal SI wall	22	173.5	114.4	30.3–784.4
Distal SI lumen	19	226.4	244.9	62.2–550.6
LI wall	22	103.3	97.4	30.1–192.8
Colon contents	22	226.6	195.6	31.2–765.8
Gastric nematodes	17	180.8	116.1	40.0–1135.6
SI acanthocephalans	18	138.7	114.3	33.1–298.5
Cestodes	14	87.5	72.1	46.3–201.5
SI nematodes	4	222.7	229.5	164.1–268.0
LI acanthocephalans	5	1227.4	1554.5	175.8–2174.3
Seals				
Liver	19	1044.5	528.1	122.4–3291.7
Kidney	19	228.1	180.8	10.2–822.6
Stomach wall	7	45.6	37.6	11.7–99.3
Stomach contents	4	49.4	45.2	12.8–94.3
Proximal SI wall	19	43.9	35.8	13.0–204.9
Proximal SI lumen	19	28.5	20.3	9.1–83.4
Distal SI wall	18	43.3	30.3	13.0–127.2
Distal SI lumen	18	43.1	33.4	8.1–137.8
LI wall	18	37.0	28.9	9.9–94.3
Colon contents	18	71.2	54.2	12.1–235.1
Gastric nematodes	6	60.4	46.7	21.7–160.3
SI acanthocephalans	18	39.8	25.8	2.6–168.9
SI nematodes	5	30.4	19.2	12.1–80.6
LI acanthocephalans	13	100.5	87.1	28.7–218.5

Table 3
Stable C, and N Isotope Values in California sea lions and seals. Stable isotope values are listed for parasites, lumen contents from different regions of the host GI tract, and host liver.

Regional lumen contents or parasite	n	Mean	Median	Range
Seals				
Nitrogen				
Stomach contents	4	16.8	17.0	15.7 to 17.7
Proximal SI lumen	7	17.0	17.1	15.6 to 18.4
dSI lumen contents	5	17.7	17.6	16.4 to 19.7
Colon contents	11	17.2	17.0	15.5 to 19.6
Gastric nematodes	5	16.0	15.3	15.1 to 17.3
SI nematodes	5	15.0	15.1	14.0 to 15.9
SI acanthocephalans	15	14.7	14.5	13.4 to 15.7
LI acanthocephalans	5	15.8	15.9	14.8 to 16.3
Carbon				
Stomach contents	4	−23.9	−24.8	−27.3 to −18.4
Proximal SI lumen	7	−24.9	−25.9	−28.7 to −20.4
dSI lumen contents	4	−22.3	−21.9	−26.1 to −19.2
Colon contents	10	−22.4	−21.2	−28.3 to −19.6
Gastric nematodes	5	−18.3	−17.7	−19.6 to −17.4
SI nematodes	5	−17.3	−17.2	−18.3 to −16.4
SI acanthocephalans	15	−19.3	−19.1	−21.0 to −17.8
LI acanthocephalans	5	−18.4	−18.7	−19.2 to −16.7
California sea lions				
Nitrogen				
Host Liver	18	18.2	18.1	17.1 to 19.0
Gastric nematodes	15	14.9	14.9	14.2 to 15.6
SI nematodes	4	15.4	14.9	14.4 to 17.4
SI cestodes	16	15.5	15.2	13.8 to 17.7
SI acanthocephalans	15	15.3	15.1	14.0 to 17.2
LI acanthocephalans	1	16.7	16.7	N/A
Carbon				
Gastric nematodes	15	−16.1	−16.4	−17.0 to −15.1
SI nematodes	4	−16.2	−16.1	−17.2 to −15.4
SI cestodes	16	−17.4	−17.3	−18.4 to −16.4
SI acanthocephalans	15	−16.9	−16.8	−18.4 to −15.9
LI acanthocephalans	1	−16.1	−16.1	N/A

mechanisms for eliminating Hg, or even demethylating $MeHg^+$ that has bioaccumulated, and further studies are needed to explore these potential adaptations.

5. Conclusion

These data confirm that parasites bioaccumulate Hg within the host GI tract. There is great variability in [THg] among parasite groups and individual species, despite the fact that there was no association between [THg] in host tissues and THg uptake by the parasites. [THg] in host tissues and lumen contents are likely being altered by the presence of parasites; and consequently, bioavailability of THg to the host may also be altered. Parasite niche within the GI tract may also be impacted, in part, by the presence of THg. The significance of these relationships requires further assessment with how well-sequestered Hg is in the parasites (not bioavailable to the host), and any role that parasites may play in demethylation or elimination of Hg. The study of mechanisms by which composition and structure of parasite infrapopulations affect the balance of ecotoxicoparasitologic interactions within the definitive host will contribute to our understanding of the effects of anthropogenic stressors on dynamic ecological systems and could help inform how these systems respond.

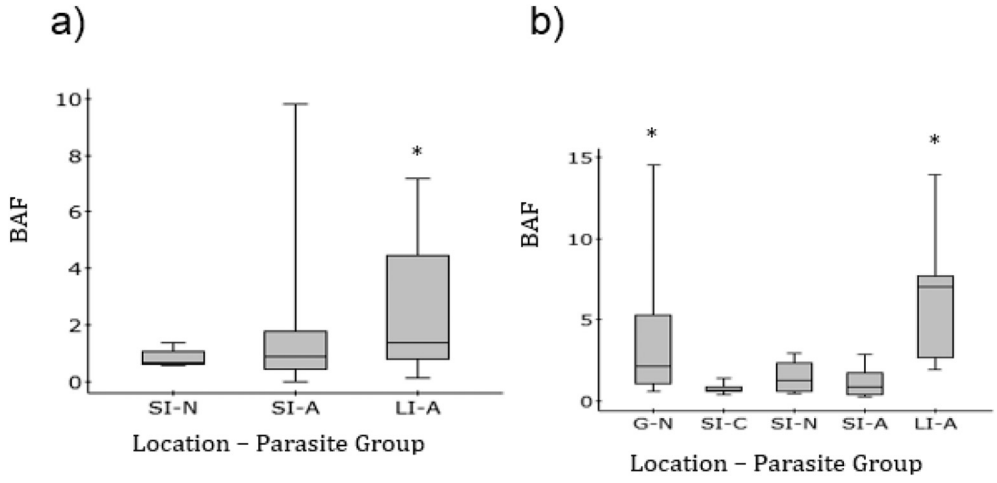

Fig. 1. BAFs in a) Seals, and b) California sea lions based on parasite group and location in the GI tract. Locations in the GI tract include gastric region (G), small intestine (SI), and large intestine (LI). Parasite groups include nematodes (N), acanthocephalans (A), and cestodes (C). Box plots display median BAFs as well as the minimum, maximum, and quartile ranges. (*) denotes groups of parasites in which the BAF lower CI was significantly higher than 1.

Acknowledgements

We are very grateful for the generosity of numerous individuals from the Native Village of Kotzebue including hunters E. Schiedt and O. Kenworthy, and thank R. Rember for her assistance with collecting samples and performing the necropsies in Kotzebue. Personnel in the Wildlife Toxicology Lab provided extensive assistance relating to instrument use, freeze-drying and weighing samples, and coordination of shipments. We appreciate the guidance and help provided by D. and S. Holcomb, S. Moses, K. Knott, L. Correa, S. Bhojwani, C. Ebner, G. Johnson, and R. Witter, and the Veterinary Services staff and volunteers of TMMC for necropsy support and assistance. We also thank B. Andre and S. Rao for their statistical consultation, and J. Cordaro of NOAA for allowing us access to marine mammal tissues. Stable isotope assistance was provided by C. Gulbransen and M. Emmons, and the authors are grateful for their guidance and expertise. We also appreciate the assistance of W. Clements, who provided valuable suggestions to an earlier version of the manuscript. The use of any trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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