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Evaluating Hair as a Predictor of Blood Mercury: The Influence of Ontogenetic Phase and Life History in Pinnipeds

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Abstract Mercury (Hg) biomonitoring of pinnipeds increasingly utilizes nonlethally collected tissues such as hair and blood. The relationship between total Hg concentrations ([THg]) in these tissues is not well understood for marine mammals, but it can be important for interpretation of tissue concentrations with respect to ecotoxicology and biomonitoring. We examined [THg] in blood and hair in multiple age classes of four pinniped species. For each species, we used paired blood and hair samples to quantify the ability of [THg] in hair to predict [THg] in blood at the time of sampling and examined the influence of varying ontogenetic phases and life history of the sampled animals. Overall, we found that the relationship between [THg] in hair and blood was affected by factors including age class, weaning status, growth, and the time difference between hair growth and sample collection. Hair [THg] was moderately to strongly predictive of current blood [THg] for adult female Steller sea lions (*Eumetopias jubatus*), adult female California sea lions (*Zalophus californianus*), and adult harbor seals (*Phoca vitulina*), whereas hair [THg] was poorly predictive or not predictive (different times of year) of blood [THg] for adult northern elephant seals (*Mirounga angustirostris*). Within species, except for very young pups, hair [THg] was a weaker predictor of blood [THg] for prereproductive animals than for adults likely due to growth, variability in foraging behavior, and transitions between ontogenetic phases. Our results indicate that the relationship between hair [THg] and blood [THg] in pinnipeds is variable and that ontogenetic phase and life history should be considered when interpreting [THg] in these tissues.

Mercury (Hg) concentrations in many marine ecosystems are increasing and have led to concern about the potential impacts of bioaccumulation in some top predators (Monteiro and Furness 1997; Sunderland and Mason 2007; Dietz et al. 2011; Mason et al. 2012). There has been an increase in ecotoxicology research and biomonitoring of Hg due to the potential negative effects of methylmercury (MeHg) on marine predators (including humans) over a wide range of Hg concentrations and periods of exposure (Ronald et al. 1984; Das et al. 2003; Finkelstein et al. 2007; Basu et al. 2009). Internal organs, such as liver and kidney, are valuable target tissues for biomonitoring because they represent Hg uptake, modified by biotransformation and sequestration processes, over the lifetime of the individual, although they typically require lethal sampling (e.g., necropsy or biosampling of animals harvested for food). As a result, there have been an increasing number of studies quantifying Hg concentrations in tissues that can be collected nonlethally.

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Nonlethally collected keratinized tissues and blood provide evidence of relatively recent exposure of animals to Hg, compared with Hg in liver and kidney, and can facilitate the direct linkage of Hg concentrations with more recent foraging behavior and current toxicological risk (Day et al. 2007; Eagles-Smith et al. 2008). In addition, total mercury (THg) in keratinized tissues and blood is almost entirely MeHg compared with liver and kidney (van de Ven et al. 1979; Soria et al. 1992; Woshner et al. 2008; Bond and Diamond 2009; Eagles-Smith et al. 2009; Dietz et al. 2011). MeHg in circulating whole blood is bioavailable, can cross the blood-brain barrier (Aschner and Aschner 1990), or be incorporated into other tissues, and it has the potential for a range of toxicological effects (Freeman and Sangalang 1977; Ronald et al. 1977; Basu et al. 2009; Dietz et al. 2013). In sled dogs, Hg in whole blood is transient on a relatively short timescale with a half-life of approximately 40–60 days (Lieske et al. 2011); thus, Hg in whole blood reflects absorption from recent meals, transfer to and between other tissues, and transformation processes within the animal. In contrast, Hg binds to proteins in feathers and hair during periods of growth and is not bioavailable to the host once the keratinized tissue is grown (Wang et al. 2014). At the time of growth, keratinized tissues can reflect circulating (e.g., blood) Hg concentrations as shown in birds and mink (Furness et al. 1986; Lewis and Furness 1991; Wang et al. 2014), although it is not clear if the strength of this relationship persists throughout the year. It can be important to understand the relationship between Hg in keratinized tissues and blood to maximize the utility of samples and guide interpretation of tissue concentrations in the context of current toxicological risk.

Keratinized tissues, such as hair and feathers, are often used for Hg research in wildlife due to the ease of collection and sample storage, limited impact of sampling to the animal, discrete growth period of these tissues in many species, and the high binding affinity of MeHg for protein-rich tissues (Harris et al. 2003; Clarkson and Magos 2006). Keratinized tissues are often used to represent Hg exposure in animals with the underlying assumption that hair or feather Hg concentrations are strongly correlated with internal tissue concentrations that directly influence current toxicological risk (Hartman et al. 2013). However, these assumptions may be contradicted when foraging behavior (e.g., location, diet), body condition (i.e., related to periods of growth or fasting), or Hg exposure changes between the time of keratinized tissue growth and the time of sampling, as shown in birds when comparing the relationship of Hg in feathers with Hg in blood (Ackerman et al. 2008, 2011; Eagles-Smith et al. 2008; Hartman et al. 2013; Lavoie et al. 2014). If the relationship between Hg in keratinized tissues and blood is decoupled due to physiological or ecological factors, then keratinized tissues and blood may provide insight into different intra-annual time periods for an individual and broaden the scope of a given study. In addition, understanding the temporal dynamics of these tissues can facilitate studies where it becomes important to make sure that individuals are directly comparable. For example, longitudinal studies of Hg in keratinized tissues have been employed in mammals and birds to show changes in Hg exposure over many years because these tissues were annually grown at the same time each year (Monteiro and Furness 1997; Dietz et al. 2006). For studies that attempt to link Hg in blood with recent foraging behavior and Hg exposure, it may be important to know if individuals sampled at different times of year can be directly compared or if there are any predictable ways to account for variability in sampling time period.

Pinnipeds, a group of marine mammals that includes seals, sea lions, fur seals, and walrus, show markedly different reproductive and molting strategies (Costa 1991), which may influence how well Hg concentrations in hair and blood represent each other. In general, pinnipeds are classified broadly into two overarching life-history strategies: income breeders and capital breeders. Income breeders forage continuously during lactation, with females alternating between periods of onshore nursing and at-sea foraging (Boness et al. 1994; Melin et al. 2000). Capital-breeding species fast during lactation, and there is often substantial geographic separation of breeding and foraging locations (Robinson et al. 2012). The duration of lactation can vary substantially within both income- and capital-breeding species, ranging from a minimum of several days to a maximum of 3 years (Costa 1991; Champagne et al. 2012). Molting strategies vary among species both in the type of molt that occurs and in the extent of fasting during the molt (Fay 1982; Ashwell-Erickson et al. 1986; Daniel 2003; Ling 2012). In contrast to species that forage while molting, some species, such as the northern elephant seal (*Mirounga angustirostris)*, fast while they undergo what is referred to as a "catastrophic molt," during which the epidermis is sloughed off with the old hair as new hair grows in over a much shorter duration than most pinnipeds (Worthy et al. 1992; Ling 2012).

Despite the increasing use of hair and blood for ecotoxicological studies and biomonitoring of Hg in pinnipeds, there have been no comprehensive studies investigating the relationship between Hg concentrations in these tissues and the factors that influence this relationship. We measured Hg in hair and blood of individuals from four eastern North Pacific pinnipeds that spanned a spectrum of ontogenetic

Table 1 Life history characteristics of age classes from four species of North Pacific pinnipeds: Steller sea lion (*E. jubatus*), California sea lion (*Z. californianus*), harbor seal (*P. vitulina*), and northern elephant seal (*M. angustirostris*)

Species	Age class	Sex	Breeding strategy[b]	Extensive fasting	Molt type[d]	Lactation duration[e]	Hair Hg source	Blood Hg source
Steller sea lion	Adult	F	Income	No	Gradual	Approximately 1 year	Prey	Prey
Steller sea lion	Juvenile	F/M	–	No	Gradual	–	Milk	Prey and milk
Steller sea lion	Old pup	F/M	–	No	Gradual	–	Gestation or milk	Milk
Steller sea lion	Young pup	F/M	–	No	Gradual	–	Gestation	Gestation and milk
California sea lion	Adult	F	Income	No	Gradual	Approximately 1 year	Prey	Prey
California sea lion	Juvenile	F/M	–	No	Gradual	–	Prey or milk	Prey
Harbor seal	Adult	F	Income	No	Gradual	3–6 weeks	Prey	Prey
Harbor seal	Adult	M	–	No	Gradual	–	Prey	Prey
Harbor seal	Juvenile	F/M	–	No	Gradual	–	Prey	Prey
Elephant seal	Adult	F	Capital	Yes[c]	Catastrophic	Approximately 26 days	Prey and body stores[c]	Prey or body stores[c]
Elephant seal	Adult	M	–	Yes[c]	Catastrophic	–	Prey and body stores[c]	Prey or body stores[c]
Elephant seal	Old pup[a]	F/M	–	No	–	–	Gestation	Gestation and milk
Elephant seal	Young pup[a]	F/M	–	No	–	–	Gestation	Gestation and milk

Molt type indicates the time period over which hair is grown: Gradual molt happens during a period of 1 to several months, whereas a catastrophic molt happens over a much shorter time period of several weeks when the hair and epidermis is sloughed off together while new hair grows in underneath

Adults were reproductive-aged animals, and juveniles were prereproductive animals >1 year old that may or may not have been independently foraging at the time of sampling, based on the species. Old pups were 2–3 months old for Steller sea lions (in the process of molting their lanugo) and 23 days for elephant seals (still had lanugo). Young pups were dependent young with lanugo and were 0.5 months old for Steller sea lions and 5 days old for elephant seals

References for life-history characteristics: Pitcher and Calkins 1981; Worthy et al. 1992; Boness et al. 1994; Le Boeuf et al. 2000; Melin et al. 2000

[a] Elephant seal pups were sampled at day 5 (young pups) and day 23 (old pups) during the approximately 26-day lactation period. They grow rapidly and do not molt their lanugo until after weaning

[b] Pinnipeds generally fall into two reproductive strategies: income breeding (foraging while lactating) and capital breeding (fasting while lactating) (Costa 1991). See the previous references for general life-history characteristics of the four study species

[c] Elephant seals have two extensive annual fasting periods, one during breeding (approximately 5–6 weeks for females and approximately 2–3 months for males) and one during molting (approximately 6 weeks)

[d] Molting in pinnipeds typically happens gradually during several months (Daniel 2003), although some species, such as the northern elephant seal, undergo a catastrophic molt that happens over a much shorter time period while the animal is fasting (Ling 2012)

[e] Lactation duration refers to the approximate length of time the adult female is lactating, although the duration is variable within each species

phases and included both capital- and income-breeding species (Table 1). We quantified Hg in hair and blood of Steller sea lions (*Eumetopias jubatus*), California sea lions (*Zalophus californianus*), harbor seals (*Phoca vitulina*), and northern elephant seals to (1) determine whether hair Hg concentrations predict blood Hg concentrations at the time of sampling; (2) evaluate the influence of varying factors, including ontogenetic phase, on the relationship between Hg concentrations in hair and blood; and (3) assess Hg concentrations in blood and hair by species and age class.

Methods

Animal Handling and Sampling

Animals were captured, restrained, and sampled using standard techniques (Jeffries et al. 1993; Le Boeuf et al. 2000; Castellini et al. 2012; McDonald and Ponganis 2013; Rea et al. 2013; McHuron et al. 2014). Sampling efforts were determined by concurrent research that restricted handling of animals to specific periods (Tables 1, 2), and some data from this article, as cited later in the text, are

presented in other publications. Steller sea lions were sampled throughout the Aleutian Islands, Gulf of Alaska, and southeast Alaska between 2000 and 2013 (Fig. 1; Castellini et al. 2012; Rea et al. 2013). California sea lions were sampled at San Nicolas, San Miguel, and Año Nuevo Islands in California between May and October 2013 (Fig. 1). Harbor seal adults and juveniles were sampled in San Francisco Bay and Elkhorn Slough in California between 2009 and 2011 (Fig. 1; McHuron et al. 2014). Northern elephant seals were sampled at Año Nuevo State Reserve, California, between 2011 and 2013 (Fig. 1) at the extremes of body condition associated with the start and end of both the breeding and molting fasts, and some individuals were sampled during multiple periods (Tables 1, 2). Paired hair and whole blood samples were collected from each animal. We determined the approximate number of months since molt for each harbor seal because they were sampled throughout the year. For Steller sea lions and northern elephant seals, we collected lanugo (natal hair) from young nursing pups. Lanugo is grown in utero and is representative of Hg concentrations to which the pup was exposed during gestation, which is thought to be the major period when female pinnipeds transfer Hg to their pups (Wagemann et al. 1988; Habran et al. 2011). Standard length was recorded for some species and age classes as a proxy for age and development (McLaren 1993). Age class definitions are listed in Table 1. Within some species, different animals were sampled at varying times throughout the year and at multiple locations.

Species-Specific Sampling

Steller Sea Lions

We sampled animals at approximately 0.5 months (young pups), 2–3 months (old pups), 14–16 months (referred to as "juveniles"), and as adult females (Table 1). Young pups were sampled before molting their lanugo coat, which happens at approximately 2 months of age (Daniel 2003), whereas old pups were sampled before and after the lanugo molt. Juveniles were sampled August to September late in a molting phase (Daniel 2003). Samples from adult females were collected late October to early November, after the annual molt.

California Sea Lions

Juvenile sea lions were sampled at San Nicolas, San Miguel, and Año Nuevo Islands in September and October of 2013, whereas adult females were sampled at San Nicolas and San Miguel Islands in May and August 2013 (Table 1). Juvenile sea lions were sampled at varying points during the annual molt; therefore, hair was recorded as either unmolted since the previous year (old), recently molted (new), or a mix of old and new hair (mixed).

Harbor Seals

Age class was determined based on length, mass, and capture date (Bigg 1969; Table 1). All prereproductive animals included in our analysis were assumed to be large enough to be independently foraging with hair that was grown while independently foraging. The majority of molting within the study region occurs in July (Harvey and Goley 2011); therefore, animals that were fully molted and captured in August were assigned a value of 1, and animals captured in June were assigned a value of 11 (with monthly increments in between), although we realize there is individual and age-class variability in the timing of molt.

Northern Elephant Seals

Adult female and male elephant seals were sampled at the two extremes of body condition, at the start and end of both the breeding (hereafter "early breeding" and "late breeding") and molting (hereafter "early molting" and "late molting") fasting periods when animals use haul-outs on land (Peterson et al. 2014; Fig. 1). Hair is entirely grown while seals are on land during the annual molt; therefore, elephant seal hair was newly grown when sampled late in the molting fast. Pups were sampled early in lactation (early breeding) at 5 to 6 days after parturition (young pups), and some of the same pups were resampled late in lactation (late breeding) at 23 days after parturition (old pups) (Table 1). Lanugo was only collected from pups early in lactation and assumed not to change during the course of the lactation period because it was grown in utero, whereas blood was sampled at early and late lactation.

Hg Analysis

We followed standard protocols for preparation of samples and quantification of total mercury concentrations ([THg]) in hair and blood (Ackerman et al. 2008; Castellini et al. 2012; Rea et al. 2013; McHuron et al. 2014). All samples were analyzed for THg using a Milestone DMA-80 direct mercury analyzer (Milestone, Monroe, Connecticut, USA) at either the United States Geological Survey Field Station Mercury Laboratory in Dixon, California, USA (California sea lions and elephant seals) or the Wildlife Toxicology Laboratory at the University of Alaska Fairbanks in Fairbanks, Alaska, USA (Steller sea lions and harbor seals). Quality-assurance measures during each run included certified reference materials, continuing calibration verifications, system and method blanks, and duplicate samples.

Table 2 Sample sizes (*N*) of four North Pacific pinniped species: Steller sea lion (*E. jubatus*), California sea lion (*Z. californianus*), harbor seal (*P. vitulina*), and northern elephant seal (*M. angustirostris*) with paired hair (dw) and whole blood (ww) Hg concentrations (μg g^{-1}) shown as mean ± SD, median, and range (in parentheses)

Species	Specific time period[a]	Tissue type	Adult female	Adult male	Juvenile female	Juvenile male	Old pup (male/female)	Young pup (male/female)	Total
Steller sea lion			(*N* = 8)	–	(*N* = 19)	(*N* = 12)	(*N* = 23)	(*N* = 195)	(*N* = 257)
		Blood	0.16 ± 0.10*	–	0.03 ± 0.02	0.03 ± 0.02	0.02 ± 0.02	0.06 ± 0.06	
			0.11*	–	0.02	0.03	0.01	0.05	
			(0.08–0.32)*	–	(< 0.01–0.05)	(< 0.01–0.07)	(< 0.01–0.09)	(0.01–0.41)	
		Hair	16.09 ± 12.86*	–	1.83 ± 0.76	1.78 ± 0.92	6.42 ± 5.24	10.76 ± 9.17	
			10.63*	–	1.89	1.49	5.32	8.39	
			(5.40–41.02)*	–	(0.86–3.18)	(0.77–3.95)	(1.30–21.26)	(2.55–73.74)	
California sea lion			(*N* = 19)	–	(*N* = 28)	(*N* = 28)	–	–	(*N* = 75)
		Blood	0.17 ± 0.08	–	0.03 ± 0.01	0.03 ± 0.01	–	–	
			0.17	–	0.03	0.03	–	–	
			(0.05–0.31)	–	(0.02–0.06)	(0.01–0.07)	–	–	
		Hair	10.56 ± 4.12	–	4.33 ± 1.76	2.41 ± 2.00	–	–	
			9.99	–	4.60	1.56	–	–	
			(5.10–21.00)	–	(1.10–7.83)	(0.74–9.57)	–	–	
Harbor seal			(*N* = 27)	(*N* = 10)	(*N* = 17)	(*N* = 16)	–	–	(*N* = 70)
		Blood	0.24 ± 0.21	0.48 ± 0.40	0.29 ± 0.16	0.21 ± 0.11	–	–	
			0.17	0.30	0.30	0.21	–	–	
			(0.06–0.90)	(0.07–1.19)	(0.07–0.78)	(0.08–0.40)	–	–	
		Hair	13.10 ± 6.60	39.85 ± 39.62	16.10 ± 9.07	16.07 ± 5.81	–	–	
			11.76	26.79	15.85	15.43	–	–	
			(5.23–26.67)	(6.27–144.31)	(2.96–36.69)	(7.98–26.02)	–	–	
Elephant seal	Late molting		(*N* = 48)	(*N* = 13)	–	–	–	–	(*N* = 61)
		Blood	0.51 ± 0.12*	0.70 ± 0.25*	–	–	–	–	
			0.52*	0.65*					
			(0.28–0.73)*	(0.34–1.14)*	–	–	–	–	
		Hair	18.74 ± 6.10*	43.68 ± 18.51*	–	–	–	–	
			18.82*	41.89*	–	–	–	–	
			(6.10–32.43)*	(14.20–75.23)*	–	–	–	–	

Table 2 continued

Species	Specific time period[a]	Tissue type	Adult female	Adult male	Juvenile female	Juvenile male	Old pup (male/female)	Young pup (male/female)	Total
Elephant seal	Early breeding		($N = 44$)	($N = 22$)	–	–	($N = 17$)	–	($N = 83$)
		Blood	0.35 ± 0.09	0.51 ± 0.24*	–	–	0.19 ± 0.05*	–	
			0.34	0.46*	–	–	0.18*	–	
			(0.18–0.60)	(0.22–1.06)*	–	–	(0.09–0.33)*	–	
		Hair	14.75 ± 5.11*	16.98 ± 10.11*	–	–	21.65 ± 6.54*	–	
			15.21*	14.44*	–	–	21.55*	–	
			(2.83–24.47)*	(5.38–39.69)*	–	–	(10.07–36.14)*	–	
Elephant seal	Late breeding		($N = 58$)	($N = 16$)	–	–	–	($N = 10$)	($N = 84$)
		Blood	0.64 ± 0.20*	0.76 ± 0.28*	–	–	–	0.09 ± 0.01*	
			0.61*	0.73*	–	–	–	0.09*	
			(0.28–1.16)*	(0.25–1.27)*	–	–	–	(0.07–0.11)*	
		Hair	16.39 ± 4.11*	12.89 ± 8.91*	–	–	–	23.22 ± 6.82*	
			16.89*	10.94*	–	–	–	22.83*	
			(4.97–23.89)*	(3.52–38.46)*	–	–	–	(13.96–36.14)*	
Elephant seal	Early molting		($N = 52$)	($N = 13$)	–	–	–	–	($N = 65$)
		Blood	0.43 ± 0.11	0.53 ± 0.20*	–	–	–	–	
			0.43	0.46*	–	–	–	–	
			(0.20–0.65)	(0.23–0.86)*	–	–	–	–	
		Hair	13.15 ± 4.00*	12.76 ± 7.78*	–	–	–	–	
			12.87*	9.77*	–	–	–	–	
			(4.79–24.82)*	(4.27–26.34)*	–	–	–	–	

Concentrations of THg are presented separately by age class and sex.

Adults were reproductive-aged animals that grew hair while independently foraging compared with animals that grew hair while dependent on maternal provisioning. Juveniles were prereproductive animals >1 year old that may or may not have been independently foraging at the time of sampling, based on the species. Old pups were 2–3 months old for Steller sea lions (in the process of molting their lanugo) and 23 days old for elephant seals (still had lanugo). Young pups were dependent young with their lanugo and were 0.5 months old for Steller sea lions and 5 days old for elephant seals

Asterisks indicate data that have not been presented elsewhere previously, and the remaining data are previously published (Castellini et al. 2012; Rea et al. 2013; McHuron et al. 2014; McHuron et al. (2015); Peterson et al. (2015)

[a] Northern elephant seals were sampled at the two extremes of body mass associated with the start and end of the two annual fasting periods (breeding and molting fasts)

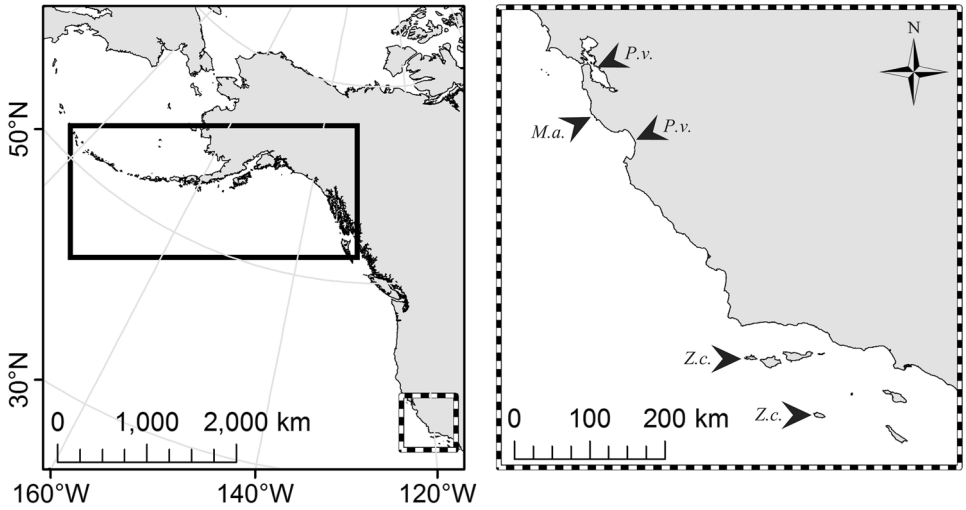

Fig. 1 Map of sampling locations of the four eastern North Pacific pinniped species sampled at terrestrial haulouts for THg in whole blood and hair: Steller sea lions (*E. jubatus*), California sea lions [*Z. californianus* (*Z. c.*)], harbor seals [*P. vitulina* (*P. v.*)], and northern elephant seals [*M. angustirostris* (*M. a.*)]. Steller sea lions were sampled throughout southeast Alaska and the Aleutian islands (shown in the large inset box within the *left panel*). California sea lions, harbor seals, and northern elephant seals were sampled within California, and arrows indicate sampling locations. Harbor seals were sampled from multiple locations in San Francisco Bay

Recoveries of standard and reference material were previously reported for harbor seals (McHuron et al. 2014) and for Steller sea lion samples collected between 2000 and 2011 (Castellini et al. 2012; Rea et al. 2013). For analysis of elephant seal and California sea lion samples, recoveries (mean ± SE) for certified reference materials from the National Research Council of Canada, Ottawa, Canada (DORM-3, DOLT-3, DOLT-4, or TORT-3) were 101.3 ± 0.5 % ($N = 75$) and for calibration verifications were 102.0 ± 0.8 % ($N = 96$). Absolute relative percent difference for sample duplicates averaged 4.3 ± 0.5 % ($N = 88$). Mercury concentrations (μg g^{-1}) are reported as $[THg]_{blood}$ wet weight (ww) for whole blood samples and $[THg]_{hair}$ dry weight (dw) for hair samples.

Overall Statistical Analysis

We performed statistical analyses using general linear models in the statistical program R version 3.1.0 (MuMIn package; R Development Core Team, Vienna, Austria) to examine how well variability in $[THg]_{hair}$ explained the variability in $[THg]_{blood}$ for the different pinniped species across a range of age classes (Table 3). We natural-log-transformed $[THg]_{hair}$ and $[THg]_{blood}$ before commencing statistical analysis to meet the assumptions of normality and homogeneity of variance. The interaction between $[THg]_{hair}$ and age class was significant for all species; therefore, we ran subsequent, more extensive analyses on all age classes separately. Age-specific models varied by species and age class based on the representation of sex, time of year, standard length, and ontogenetic phases within an age class (e.g., weaning status) in the datasets for the four different species (Table 3). Full and reduced models were compared using Akaike Information Criterion adjusted for small sample sizes (AIC_c), and models within a ΔAIC_c value of 2 were further examined to select the most parsimonious model (Burnham et al. 2011). If the best model contained variables other than $[THg]_{hair}$ to explain the variability in $[THg]_{blood}$, we calculated evidence ratios between the best model and the model without the additional variable. We used the adjusted r^2 value from the best model to characterize the predictive ability: $r^2 \leq 0.35$ had little predictive ability; $0.36 < r^2 < 0.55$ was weakly predictive; $0.56 < r^2 < 0.75$ was moderately predictive; and $r^2 > 0.75$ was strongly predictive (O'Hara et al. 2008). Regression equations for the best models with adjusted $r^2 \geq 0.35$ are listed in Table 4.

Species-Specific Statistical Analyses

Steller Sea Lions

We ran a full model with all prereproductive age classes together to examine if there was an interaction between prereproductive age class and $[THg]_{hair}$. The interaction was significant, which further justified separate analysis for each prereproductive age class. The full model for young pups included $[THg]_{hair}$, sex, standard length, and an interaction between $[THg]_{hair}$ and sex. The full model for old pups was the same as for young pups with the addition of molt status and an interaction between $[THg]_{hair}$ and molt status. The full model for juveniles was the same as

Table 3 Model comparison, by age class, for four North Pacific pinniped species—Steller sea lion (*E. jubatus*), California sea lion (*Z. californianus*), harbor seal (*P. vitulina*), and northern elephant seal (*M. angustirostris*)—to explain the variability in $[THg]_{blood}$ using $[THg]_{hair}$ and other variables including sex, standard length (length), molt status (molt) and weaning status (weaning)

Species Specific time period	Age class	Models	k	logLik	AIC_c	ΔAIC_c	w_i	r^2 adj
Steller sea lion	Adult	THg_{hair}	**3**	**6.24**	**−0.5**	**0.0**	**0.94**	**0.95**
		*THg_{hair} + length	4	8.10	5.1	5.6	0.06	0.96
		Length	3	−3.43	18.9	19.4	0.00	0.45
		Intercept only	2	−6.43	19.3	19.8	0.00	0.00
Steller sea lion	Juvenile (14–16 months)	THg_{hair} + weaning	**4**	**−18.37**	**46.3**	**0.0**	**0.23**	**0.71**
		THg_{hair} + length + weaning	5	−17.05	46.5	0.2	0.21	0.72
		THg_{hair} + length + weaning + sex	6	−15.78	47.1	0.8	0.16	0.74
		THg_{hair} + length + weaning + sex + THg_{hair} × sex	6	−16.48	48.5	2.2	0.08	0.72
		*THg_{hair} + length + weaning + sex + THg_{hair} × sex + THg_{hair} × weaning	8	−14.80	52.1	5.8	0.01	0.73
		THg_{hair}	3	−27.07	61.0	14.7	0.00	0.51
		Intercept only	2	−35.59	81.6	35.3	0.00	0.00
Steller sea lion	Old pup (2–3 months)	THg_{hair} + molt	**4**	**−6.80**	**23.8**	**0.0**	**0.54**	**0.79**
		THg_{hair} + molt + sex	5	−6.49	26.5	2.7	0.14	0.78
		THg_{hair} + molt + THg_{hair} × molt	5	−6.72	27.0	3.2	0.11	0.78
		THg_{hair} + molt + length	5	−6.80	27.1	3.3	0.10	0.77
		*THg_{hair} + sex + THg_{hair} × sex + molt + THg_{hair} × molt + length	8	−6.07	38.4	14.6	0.00	0.75
		THg_{hair}	3	−16.09	39.45	15.6	0.00	0.54
		Intercept only	2	−25.56	55.7	31.9	0.00	0.00
Steller sea lion	Young pup (0.5 month)	THg_{hair} + length	**4**	**−44.30**	**96.8**	**0.0**	**0.52**	**0.78**
		THg_{hair} + length + sex	5	−43.66	97.6	0.8	0.35	0.78
		*THg_{hair} + length + sex + THg_{hair} × sex	6	−43.55	99.5	2.7	0.13	0.78
		THg_{hair}	3	−52.45	111.0	14.2	0.00	0.76
		Intercept only	2	−192.07	388.2	291.4	0.00	0.00
California sea lion	Adult	THg_{hair}	**3**	**−4.66**	**16.9**	**0.0**	**0.81**	**0.61**
		*THg_{hair} + length	4	−4.49	19.8	2.9	0.19	0.60
		Intercept only	2	−14.06	32.9	16.0	0.00	0.00
		Length	3	−13.30	34.2	17.3	0.00	0.23
California sea lion	Juvenile	THg_{hair} + molt + THg_{hair} × molt	**7**	**−15.82**	**48.0**	**0.0**	**0.33**	**0.24**
		THg_{hair}	3	−21.44	49.3	1.3	0.16	0.14
		THg_{hair} + molt + THg_{hair} × molt + sex	8	−15.25	49.6	1.6	0.15	0.24
		THg_{hair} + molt	5	−19.58	50.4	2.4	0.10	0.17
		*THg_{hair} + molt + THg_{hair} × molt + sex + THg_{hair} × sex	9	−14.23	50.4	2.4	0.10	0.25
		Intercept only	2	−26.26	56.7	8.7	0.00	0.00

Table 3 continued

Species Specific time period	Age class	Models	k	logLik	AIC_c	ΔAIC_c	w_i	r^2 adj
Harbor seal	Adult	THg_{hair} + month	**4**	**−2.99**	**15.2**	**0.0**	**0.35**	**0.90**
		THg_{hair} + month + sex + THg_{hair} × sex	6	−0.69	16.2	1.0	0.22	0.90
		THg_{hair} + month + sex	5	−2.27	16.5	1.3	0.19	0.90
		THg_{hair} + month + THg_{hair} × month	5	−2.73	17.7	2.5	0.10	0.90
		*THg_{hair} + month + sex + THg_{hair} × sex + length	7	−0.11	18.1	2.9	0.09	0.90
		THg_{hair}	3	−14.96	36.6	71.9	0.00	0.81
		Intercept only	2	−46.31	97.0	81.8	0.00	0.00
Harbor seal	Juvenile	THg_{hair} + month	**4**	**−12.77**	**35.0**	**0.0**	**0.41**	**0.64**
		THg_{hair} + month + sex	5	−11.89	36.0	1.0	0.24	0.66
		THg_{hair} + month + sex + THg_{hair} × sex	6	−11.02	37.3	2.3	0.13	0.68
		THg_{hair} + month + length	5	−12.77	37.8	2.8	0.10	0.64
		*THg_{hair} + month + sex + THg_{hair} × sex + length	7	−10.60	39.7	4.7	0.04	0.63
		THg_{hair}	3	−23.36	53.6	18.6	0.00	0.30
		Intercept only	2	−29.68	63.8	28.8	0.00	0.00
Elephant seal (*late molting*)	Adult	THg_{hair}	**3**	**3.93**	**−1.4**	**0.0**	**0.58**	**0.41**
		THg_{hair} + sex	4	4.14	0.4	2.0	0.23	0.41
		*THg_{hair} + sex + THg_{hair} × sex	5	5.18	0.7	2.1	0.20	0.42
		Sex	3	−8.22	22.9	24.3	0.00	0.13
		Intercept only	2	−12.78	29.8	31.2	0.00	0.00
Elephant seal (*early breeding*)	Adult	*THg_{hair} + sex + THg_{hair} × sex	**5**	**−12.17**	**35.3**	**0.0**	**0.50**	**0.31**
		THg_{hair} + sex	4	−13.36	35.4	0.1	0.49	0.30
		THg_{hair}	3	−19.07	44.5	9.2	0.01	0.18
		Sex	3	−20.78	47.9	12.6	0.00	0.13
		Intercept only	2	−25.95	56.1	20.8	0.00	0.00
Elephant seal (*late breeding*)	Adult	THg_{hair} + sex	**4**	**−14.56**	**37.7**	**0.0**	**0.72**	**0.26**
		*THg_{hair} + sex + THg_{hair} × sex	5	−14.36	39.6	1.9	0.28	0.25
		THg_{hair}	3	−20.17	46.7	9.0	0.01	0.15
		Intercept only	2	−26.51	57.2	19.5	0.00	0.00
		Sex	3	−25.54	57.4	19.7	0.00	0.01
Elephant seal (*early molting*)	Adult	THg_{hair} + sex	**4**	**−9.97**	**28.6**	**0.0**	**0.60**	**0.12**
		*THg_{hair} + sex + THg_{hair} × sex	5	−9.90	30.8	2.2	0.20	0.11
		THg_{hair}	3	−12.79	32.0	3.4	0.11	0.05
		Sex	3	−13.33	33.0	4.4	0.07	0.04
		Intercept only	2	−15.12	34.4	5.8	0.03	0.00

Table 3 continued

Species Specific time period	Age class	Models	k	logLik	AIC_c	ΔAIC_c	w_i	r^2 adj
Elephant seal (*late breeding*)	Old pup	*THg_{hair}	**3**	**7.29**	**−4.6**	**0.0**	**0.59**	**0.32**
	(23 days)	Intercept only	2	4.76	−3.8	0.8	0.41	0.00
Elephant seal (*early breeding*)	Young pup	*THg_{hair}	**3**	**8.34**	**−8.8**	**0.0**	**1.00**	**0.69**
	(5 days)	Intercept only	2	−2.17	9.2	18.0	0.00	0.00

General linear models were run on natural-log-transformed $[THg]_{blood}$ and $[THg]_{hair}$. Listed models are either the best four models or all models with $\Delta AIC_c \leq 2$ in addition to the full model (indicated by Asterisk), the model with just $[THg]_{hair}$, and the intercept-only model. The best model is in bold

Statistical abbreviations for the models include the following: k (number of parameters), logLik (log likelihood), AIC_c (Akaike Information Criterion adjusted for small sample sizes), w_i (Akaike weights), and r^2 *adj* (adjusted r^2)

Adults are reproductive aged animals, and juveniles are prereproductive animals > 1 year old

Molt for Steller sea lions is molted or unmolted and for California sea lions is old hair, mixed new and old hair, or new hair

Weaning status for Steller sea lions is whether or not they have weaned at the time of sampling

Models for elephant seals, the species that fasts during breeding and molting, are listed separately by the specific time period of sampling (in italics)

for young pups with the addition of weaning status (determined by whisker isotope analysis Rea et al. 2015) and an interaction between $[THg]_{hair}$ and weaning status. For adult females, the only variables in the full model were $[THg]_{hair}$ and standard length.

California Sea Lions

For prereproductive animals, we included $[THg]_{hair}$, sex, molt status (old, new, or mixed hair), and an interaction between $[THg]_{hair}$ and molt status as possible explanatory variables. We added standard length to the separate analysis for adult females. It should be noted that samples from adult females did not represent multiple molt phases, and thus this variable was not examined for adult females.

Harbor Seals

Factors included in the full models for adults and juveniles included $[THg]_{hair}$, sex, the number of months since molt, and an interaction between $[THg]_{hair}$ and sex. Harbor seals were the only nonfasting species in our study with animals sampled throughout the year, which allowed us to examine the potential influence of the time since the growth of new hair on the relationship between $[THg]_{blood}$ and $[THg]_{hair}$.

Northern Elephant Seals

We examined the four distinct times of year separately because of the extreme differences in physiology between the time periods due to fasting on land in addition to having some individuals that were sampled at multiple time periods. Factors included in the full model for adult seals were $[THg]_{hair}$, sex, and an interaction between $[THg]_{hair}$ and sex. For elephant seal pups, we separately analyzed samples from early and late breeding.

Results

Overview of Tissue [THg]

Hair and blood [THg] in the four species spanned a wide range of values from 0.74 to 144.31 μg g^{-1} dw in hair and <0.01 to 1.19 μg g^{-1} ww in blood (Table 2). Overall, adult northern elephant seals had the greatest median hair and blood [THg], although the greatest absolute concentrations in both tissues were from a harbor seal (Table 2). Although samples in our study were collected from adult females of all four species at varying times within a year, making it complicated to compare them directly, median $[THg]_{blood}$ was ≥0.34 μg g^{-1} ww for northern elephant seals (for all four different time periods within a year when

Table 4 Model equations for the best model to predict $[THg]_{blood}$ from $[THg]_{hair}$ with additional variables for four species of pinnipeds: Steller sea lion (*E. jubatus*), California sea lion (*Z. californianus*), harbor seal (*P. vitulina*), and northern elephant seal (*M. angustirostris*)

Species	Age class	Model equation
Steller sea lion	Adult	$\ln[THg]_{blood} = -3.9355 + (\ln[THg]_{hair}) \times 0.7670$
	Juvenile (nursing)	$\ln[THg]_{blood} = -4.8317 + (\ln[THg]_{hair}) \times 0.8012$
	Juvenile (weaned)	$\ln[THg]_{blood} = -4.8317 + (\ln[THg]_{hair}) \times 0.8012 + 0.9139$
	Old pup (unmolted)	$\ln[THg]_{blood} = -4.6439 + (\ln[THg]_{hair}) \times 0.4875$
	Old pup (molted)	$\ln[THg]_{blood} = -4.6439 + (\ln[THg]_{hair}) \times 0.4875 - 0.8424$
	Young pup	$\ln[THg]_{blood} = -3.3238 + (\ln[THg]_{hair}) \times 0.9367 - 0.0157 \times$ length
California sea lion	Adult	$\ln[THg]_{blood} = -4.3057 + (\ln[THg]_{hair}) \times 1.0485$
Harbor seal	Adult	$\ln[THg]_{blood} = -4.9159 + (\ln[THg]_{hair}) \times 1.0598 + 0.1008 \times$ month
	Juvenile	$\ln[THg]_{blood} = -3.9481 + (\ln[THg]_{hair}) \times 0.6488 + 0.1408 \times$ month
Elephant seal	Young pup	$\ln[THg]_{blood} = -3.9769 + (\ln[THg]_{hair}) \times 0.7441$

Equations are only shown for the models with adjusted $r^2 \geq 0.35$

Separate equations are shown for categorical variables (e.g., nursing vs. weaned juvenile Steller sea lions). Continuous variables are length (cm) and months (integer months since molting, starting with August as month 1 and June as month 11)

Adults were reproductive-aged animals, and juveniles were prereproductive animals >1-year-old. Juvenile Steller sea lions were in the process of transitioning to independent foraging (nursing vs. weaned). All pups were nursing at the time of tissue sampling. Old pups were 2–3 months old for Steller sea lions [in the process of molting their lanugo (unmolted vs. molted)] and 23 days old for elephant seals (still had lanugo). Young pups all had lanugo and were 0.5 months old for Steller sea lions and 5 days old for elephant seals

we sampled), 0.17 μg g^{-1} ww for harbor seals, 0.17 μg g^{-1} ww for California sea lions, and 0.11 μg g^{-1} ww for Steller sea lions (Table 2). Median $[THg]_{hair}$ was similar for adult females of all four species: northern elephant seals had ≥12.87 μg g^{-1} dw (at the four different time periods); harbor seals had 11.76 μg g^{-1} dw; California sea lions had 9.99 μg g^{-1} dw;, and Steller sea lions had 10.63 μg g^{-1} dw (Table 2). In contrast, median $[THg]_{hair}$ was ≥9.77 μg g^{-1} for adult male northern elephant seals (for all four different time periods within a year when we sampled) and 26.79 μg g^{-1} for adult male harbor seals (Table 2). Except for harbor seals, adults generally had greater ranges and greater median concentrations of THg than juveniles and old pups within each species, although young Steller sea lion and northern elephant seal pups had [THg] in hair and blood that substantially overlapped with [THg] observed in adult female tissues (Table 2).

Relationship Between Hair and Blood [THg]

In general, $[THg]_{blood}$ in all four species increased with $[THg]_{hair}$, but the explanatory power of $[THg]_{hair}$ for predicting $[THg]_{blood}$ varied substantially among species and was influenced by factors including ontogenetic phase and the timing of sampling (Table 3). Hair [THg] was moderately to strongly predictive of $[THg]_{blood}$ for adult Steller sea lions, California sea lions, and harbor seals (adj $r^2 > 0.60$), whereas $[THg]_{hair}$ was poorly predictive or had no predictive value for $[THg]_{blood}$ in northern elephant seals (adj $r^2 \leq 0.41$) (Fig. 2a–d). Within a species, the predictive power of the best model was generally higher in adult compared with prereproductive age classes, with the exception of northern elephant seals, where the predictive power in adults was particularly low.

The best model for predicting [THg] in blood of adult female Steller sea lions included only $[THg]_{hair}$ and was strongly predictive (adj $r^2 > 0.95$), whereas the best models for all prereproductive age classes of Steller sea lions each had one additional variable in the best model and were moderately to strongly predictive (Table 3). The best model for juveniles included weaning status (evidence ratio = 1589), whereas the best model for old pups included molt status (evidence ratio = 2484), and the best model for young pups included standard length (evidence ratio = 1219) (Table 3). Based on the equation for the best model, for animals with the same $[THg]_{hair}$, weaned juveniles had approximately 50 % higher $[THg]_{blood}$ than animals that were still nursing (Fig 3a; Tables 2, 3). Old pups that had molted their lanugo had approximately 57 % lower $[THg]_{blood}$ than unmolted animals with the same $[THg]_{hair}$. Young pup $[THg]_{blood}$ decreased approximately 15 % for each 10 cm increase in standard length for animals with the same $[THg]_{hair}$ (Tables 2, 3). The model with only $[THg]_{hair}$ was strongly predictive for young pups (adj $r^2 = 0.76$) but was only weakly predictive of $[THg]_{blood}$ for old pups and older juveniles (adj $r^2 = 0.54$ and 0.51, respectively; Table 3). Sex and interactions between $[THg]_{hair}$ and sex, weaning status, or molting status were uninformative variables for all of the prereproductive age classes (Table 3). The ΔAIC_c between the best models and the null model was >19.8.

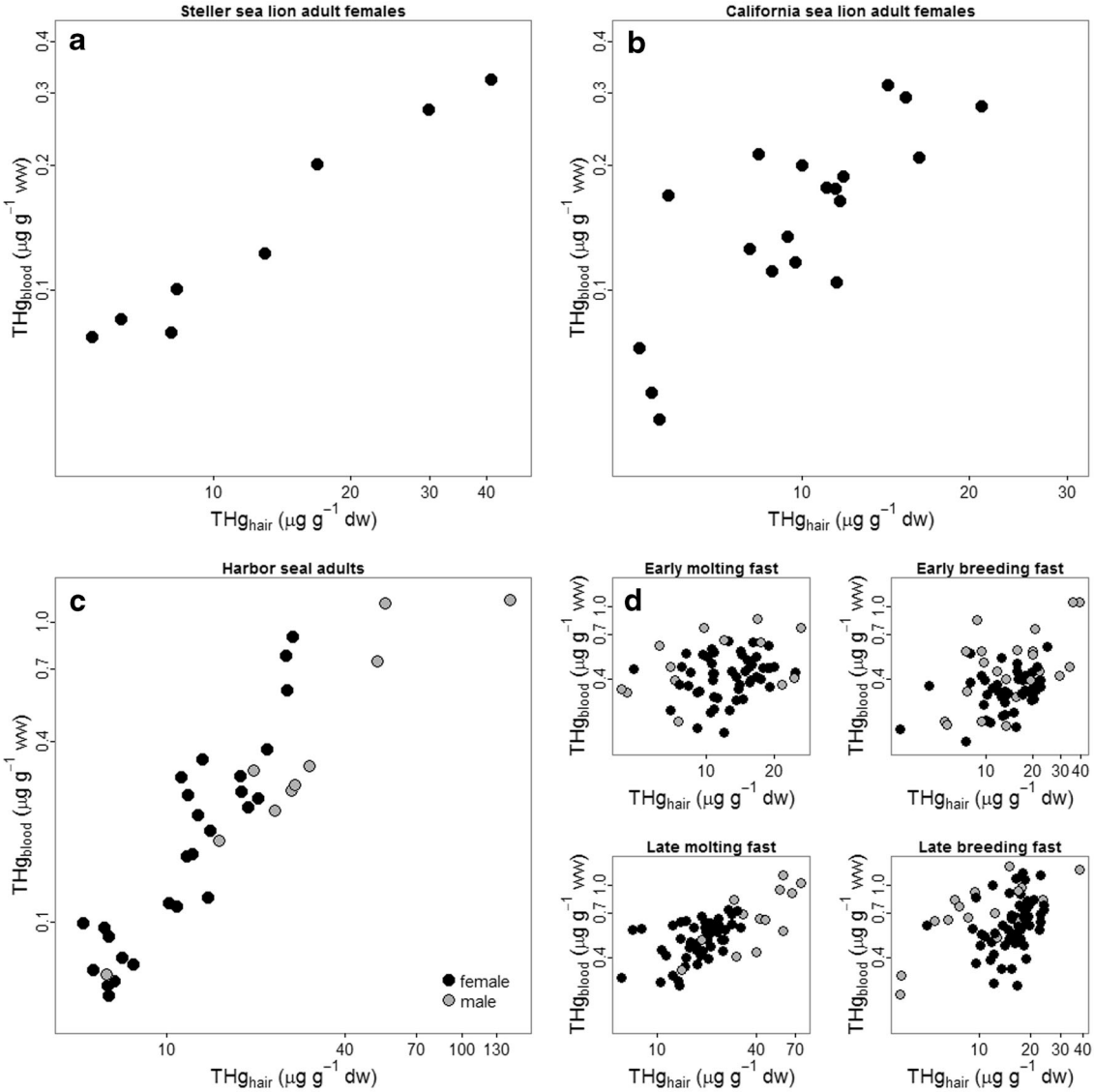

Fig. 2 The ability of $[THg]_{hair}$ to predict current circulating $[THg]_{blood}$ varied among adults from four species of pinnipeds: Steller sea lions (*E. jubatus*), California sea lions (*Z. californianus*), harbor seals (*P. vitulina*), and northern elephant seals (*M. angustirostris*). Female and male harbor seals and elephant seals are represented using black (females) and gray (males). Untransformed data are presented using $\log_{10}$-scaled axes that vary among the panels. **a** $[THg]_{hair}$ was strongly predictive of $[THg]_{blood}$ in adult female Steller sea lions (adj $r^2 = 0.95$). **b** $[THg]_{hair}$ was moderately predictive of $[THg]_{blood}$ in adult female California sea lions (adj $r^2 = 0.61$). **c** $[THg]_{hair}$ and the number of months since molt was strongly predictive of $[THg]_{blood}$ in harbor seals (adj $r^2 = 0.90$). **d** $[THg]_{hair}$ was poorly predictive of $[THg]_{blood}$ in adult northern elephant seals when the hair was brand new (late molting fast; *adj* $r^2 = 0.41$) but was not predictive at all other times of the year

The best model to explain $[THg]_{blood}$ in adult female California sea lions included only $[THg]_{hair}$ and was moderately predictive (adj $r^2 = 0.61$). The best model for juveniles included $[THg]_{hair}$, molt status (newly grown, mixed new and old, or old hair), and an interaction between $[THg]_{hair}$ and molt status, and had no predictive value (adj $r^2 = 0.24$; Table 3). Evidence ratios indicated that the best model for juveniles was only three times more likely than the model without the $[THg]_{blood} \times$ molt status interaction and only twice as likely as a model without molt status. The ΔAIC_c between the best model for both age groups and the null model was >8.

The best models for adult and juvenile harbor seals both included $[THg]_{hair}$ and the time since molt (in months) (Tables 2, 3; Fig 4). The combination of $[THg]_{hair}$ and the time since molt was strongly predictive of $[THg]_{blood}$ for adults (adj $r^2 = 0.90$), whereas those same variables were moderately predictive of $[THg]_{blood}$ for juveniles (adj

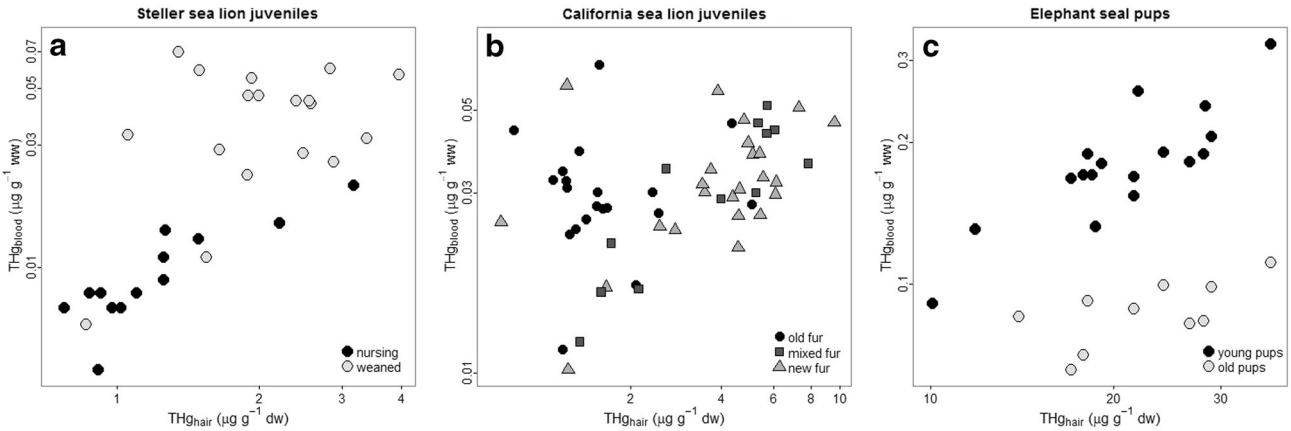

Fig. 3 The influence of different ontogenetic phases on the relationship between $[THg]_{hair}$ and $[THg]_{blood}$. Untransformed data are presented using log_{10}-scaled axes that vary among the panels. **a** The best model for juvenile (prereproductive animals >1 year old) Steller sea lions (*E. jubatus*) included $[THg]_{hair}$ and weaning status (i.e., transitioning from nursing to independent foraging) and was moderately predictive of $[THg]_{blood}$ (adj $r^2 = 0.71$). **b** The best model for juvenile California sea lions (*Z. californianus*) included $[THg]_{hair}$ and molt status (old hair from the previous molt, mixed new and old hair, and new hair from a recent molt), but it had no predictive value (adj $r^2 = 0.24$) for $[THg]_{blood}$. **c** The best model for northern elephant seal (*M. angustirostris*) pups early in lactation included only $[THg]_{hair}$ and moderately predicted $[THg]_{blood}$ (adj $r^2 = 0.69$), but it had no predictive value (adj $r^2 = 0.32$) late in lactation (when pups were near weaning)

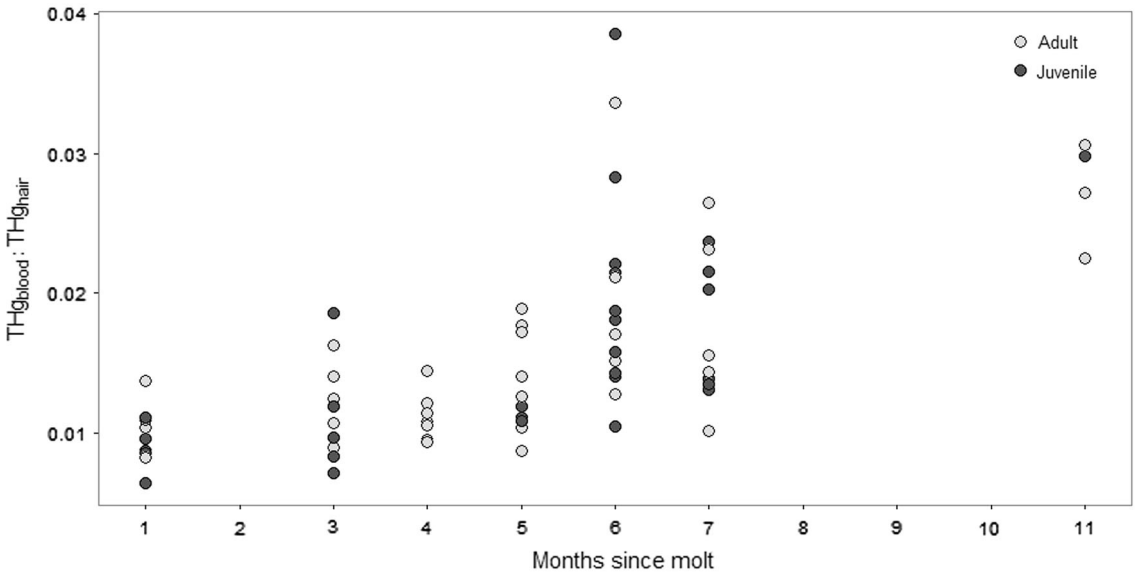

Fig. 4 The temporal increase in $[THg]_{blood}$, relative to $[THg]_{hair}$ with time since molt, shown here as the $[THg]_{blood}$-to-$[THg]_{hair}$ ratio, for adult and juvenile (weaned prereproductive animals >1 year old) harbor seals (*P. vitulina*). One seal was omitted from representation here due to a large ratio but was included in the statistical analysis

$r^2 = 0.62$). Based on calculated evidence ratios, the best models were approximately 4.4×10^4 and 1.1×10^4 times more likely than the models without time since molt for adults and juveniles, respectively. Hair [THg] alone was strongly predictive of $[THg]_{blood}$ in adults (adj $r^2 = 0.81$) but was not predictive for juveniles (adj $r^2 = 0.30$; Table 3; Fig 2b). Sex, standard length, and the $[THg]_{hair} \times$ sex interaction were all uninformative parameters (Table 3). The ΔAIC_c between the best model and the null model for both age classes was >28.

With the exception of young pups, none of the best models for northern elephant seals were more than weakly predictive of $[THg]_{blood}$. When the hair was newly grown (at the end of the annual molt), $[THg]_{hair}$ was weakly predictive of $[THg]_{blood}$ (adj $r^2 = 0.41$); however, $[THg]_{hair}$ had no predictive value at all other times of year (adjusted $r^2 \leq 0.31$; Table 3). At all time periods, except for when the hair was newly formed, the best model for adult elephant seals included $[THg]_{hair}$ and sex, indicating that male elephant seals had higher $[THg]_{blood}$ than female

seals for the equivalent $[THg]_{hair}$ (Table 3). Based on calculated evidence ratios, the best model at early breeding, late breeding, and early molting was 99, 89, and 5 times more likely, respectively, than the model with only $[THg]_{hair}$ (Table 3). The $[THg]_{hair} \times$ sex interaction improved the model during early breeding, indicating that the slope of the $[THg]_{hair}$ and $[THg]_{blood}$ relationship varied by sex and was slightly steeper for males, but this interaction was considered an uninformative variable at other time periods. The null models for all sampling periods had a ΔAIC from the best model between 5.8 and 31.2.

The relationship between $[THg]_{hair}$ and $[THg]_{blood}$ in northern elephant seal pups substantially changed between the start (5 days after parturition) and end (23 days after parturition) of the approximately 26-day lactation period. Early in lactation, $[THg]_{hair}$ was moderately predictive of $[THg]_{blood}$ (adj $r^2 = 0.69$), but $[THg]_{hair}$ had no predictive value (adj $r^2 = 0.32$) late in lactation (Tables 2, 3; Fig. 2c). The ΔAIC between the best model and the null model was 18.0 early in lactation but decreased to 0.8 late in lactation.

Discussion

The four North Pacific pinniped species we examined had $[THg]_{hair}$ and $[THg]_{blood}$ spanning the typical range of tissue concentrations (hair = 0.74–144.31 μg g^{-1} dw; blood = <0.01–1.19 μg g^{-1} ww) in other pinniped species including Baikal seals (*Pusa sibirica*), Caspian seals (*Pusa caspica*), northern fur seals (*Callorhinus ursinus*), Weddell seals (*Leptonychotes weddellii*), ringed seals (*Pusa hispida*), and bearded seals (*Erignathus barbatus*) (Ikemoto et al. 2004; Gray et al. 2008; Table 2). In addition, our study included a broad spectrum of age classes, ontogenetic phases, varying life history strategies, and both sexes, thus making it more comprehensive than any previous study for understanding the relationship between [THg] in hair and blood of pinnipeds.

Interpretation of tissue concentrations regarding current toxicological risk depends on the relationship between the [THg] in sampled tissues and [THg] in tissues that directly influence risk (Hartman et al. 2013). The utility of $[THg]_{hair}$ to predict the circulating $[THg]_{blood}$ at the time of sampling varied substantially among and within species, and was influenced by a number of factors. If there is a strong relationship between $[THg]_{hair}$ and $[THg]_{blood}$, then both tissues should relate similarly to recent foraging behavior and current toxicological risk. Conversely, if $[THg]_{hair}$ and $[THg]_{blood}$ are not strongly related at the time of collection, then interpretation of current toxicological risk becomes difficult. If [THg] in hair and blood are not strongly related at the time of sampling and/or represent Hg exposure at different time periods, then sampling both keratinized and circulating tissues may be useful to quantify Hg exposure and toxicological risk at varying temporal scales and/or from potentially different sources (gestation vs. lactation vs. independent foraging).

In three of the four species, the relationship between [THg] in hair and blood in the adult pinnipeds was moderately to strongly predictive. For juveniles, very young Steller sea lion and elephant seal pups also had moderately to strongly predictive relationships between $[THg]_{hair}$ and $[THg]_{blood}$. The decreased strength of the $[THg]_{hair}$ and $[THg]_{blood}$ relationship in northern elephant seals and some prereproductive age classes from other species suggests that these two tissues are not always reliable predictors of each other at the time of sampling. The strength of the relationship for some species was affected by age class, ontogenetic phase within an age class (e.g., weaning status, molting status), growth, and time of year, thus indicating that these are important factors to consider when interpreting [THg] in hair and blood.

In general, the strength of the relationship between $[THg]_{hair}$ and $[THg]_{blood}$ was stronger and more consistent in species and age classes with less intra-annual variability in foraging behavior, in which case either tissue could be used to link [THg] with recent behavior and current toxicological risk. Adult harbor seals and female sea lions do not have extended fasting periods associated with breeding or molting (Pitcher and Calkins 1981; Boness et al. 1994; Melin et al. 2000; Williams et al. 2007), and all had $[THg]_{hair}$ that moderately to strongly predicted the circulating pool of Hg in the blood. In contrast, northern elephant seals fast for extensive periods of time during both of these time periods (Costa et al. 1986; Worthy et al. 1992) and $[THg]_{hair}$ was a poor predictor of $[THg]_{blood}$ in northern elephant seals when hair was new (i.e., late molting), and it had no predictive value at all other times of year (Table 3). In addition, the catastrophic molt of elephant seals may contribute to the poor relationship between [THg] in hair and blood. Hair may still be a useful matrix to predict toxicological risk in this species because it is representative of blood [THg] at some point during the molt, but the inability of hair to predict blood [THg] during the majority of the year indicates that hair [THg] should not be linked with recent foraging behavior.

In addition to differences in the strength of the predictive relationship among adults of the four species, we observed differences in the predictive relationship between adults and juveniles within a given species. Juvenile harbor seals and sea lions had weaker relationships between $[THg]_{hair}$ and $[THg]_{blood}$ than adults, which could potentially be explained by a combination of more variable foraging behavior in juveniles throughout the year as well as other factors including more rapid growth in younger

age classes and the transition from maternal provisioning to independent foraging (Merrick and Loughlin 1997; Lowry et al. 2001).

The potential influence of sex on the relationship between $[THg]_{hair}$ and $[THg]_{blood}$ was not found to improve the ability of $[THg]_{hair}$ to predict $[THg]_{blood}$. For example, the best model to explain variability in $[THg]_{blood}$ in northern elephant seals included sex at all time periods except for when the hair was brand new (late in the molt after a prolonged fasting period). However, even the best models with $[THg]_{hair}$ and sex had no predictive value for $[THg]_{blood}$ (Table 3). Sex was not a predictor of the relationship between $[THg]_{hair}$ and $[THg]_{blood}$ in harbor seals, but it may still be important in pinnipeds with different life-history strategies. For example, male and female harbor seals are similarly sized, nonmigratory, and assumed to feed relatively continuously throughout the year (Boness et al. 1994; Coltman et al. 1997). In contrast, sea lions are sexually dimorphic, typical of otariids, and adult males can spend more than 1 month fasting during the breeding season (Gentry 1971), whereas adult females continue to foraging throughout lactation (Costa 1991; Melin et al. 2000). The influence of fasting on blood [THg] (Habran et al. 2010), in addition to other possible differences in foraging behavior (e.g., foraging location, diet), make it probable that the relationship between $[THg]_{hair}$ and $[THg]_{blood}$ would differ at specific times of year between the sexes of adult animals from some pinniped species, such as otariids, but our study could not test this hypothesis.

The relationship between Hg in hair and blood varied temporally as a result of changing $[THg]_{blood}$. Among all species and age classes, the relationship between $[THg]_{hair}$ and $[THg]_{blood}$ was strongest for adult female Steller sea lions, which were sampled just after their annual molt. In harbor seals that were sampled throughout the year, time elapsed since hair growth was important in best explaining the relationship between $[THg]_{hair}$ and $[THg]_{blood}$ (Table 3; Fig. 4). Blood [THg] was lowest right after the annual molt, which was likely a result of Hg depuration into the hair. A similar trend has been observed in avian studies, where sequestration of Hg into feathers during the molt resulted in decreased $[THg]_{blood}$ (Braune 1987; Bearhop et al. 2000). In harbor seals, the temporal increase in $[THg]_{blood}$ relative to $[THg]_{hair}$ with increasing time since the molt may indicate offloading during the molting period followed by bioaccumulation of Hg between molting periods, similar to the offloading of THg into hair observed in mink (Wang et al. 2014). We would also expect to see this relationship in other continuously foraging pinniped species, although the magnitude of change might vary depending on the level and consistency of environmental Hg exposure and the duration of molt. Our observations suggest that $[THg]_{hair}$ in nonmigratory pinnipeds with consistent foraging behavior is likely moderately predictive of $[THg]_{blood}$ for animals sampled throughout the year.

Growing animals move through a suite of ontogenetic phases, at which point other factors in addition to $[THg]_{hair}$ become important to explain the variability in $[THg]_{blood}$. For example, when nursing Steller sea lion pups (old pups) molted their lanugo, molt status became important in explaining the variability in $[THg]_{blood}$, likely because $[THg]_{blood}$ was lower after molting due to the removal of Hg from blood during the growth of new hair. When Steller sea lions transitioned to independent foraging, weaning status became important to explain the variability in $[THg]_{blood}$. Before weaning, but after molting of the lanugo, relatively low $[THg]_{hair}$ and $[THg]_{blood}$ likely resulted from low Hg concentrations delivered in lipid-rich milk during lactation (Tables 1, 2; Habran et al. 2011). Therefore, after weaning, hair continues to reflect the low-Hg diet of nursing pups until the next molt, but blood will gradually reflect the often higher [THg] in protein-rich marine prey (Fig. 3a). Despite our moderate to strong ability to predict $[THg]_{blood}$ from $[THg]_{hair}$ in juvenile Steller sea lions and harbor seals (with the inclusion of other variables), $[THg]_{hair}$ was not predictive of $[THg]_{blood}$ in juvenile California sea lions. This may have been partially attributed to the fact that this age class included both yearlings and older juveniles as a result of the difficulty in the field to accurately distinguish free-ranging yearling animals from 2-year-olds. Consequently, $[THg]_{blood}$ in juvenile California sea lions should have represented independent foraging, although some animals likely grew hair while nursing, whereas others had grown hair while independently foraging (Fig. 3b).

Rapid growth of developing animals can also cause a dilution of [THg] in blood (Sakamoto et al. 2002; Ackerman et al. 2011; Habran et al. 2011) and other compartments that do not have fixed [THg], which may have influenced some of the relationships we observed. In elephant seal pups, rapid growth likely explains, in part, why Hg concentrations in lanugo (grown in utero) were moderately predictive of $[THg]_{blood}$ early in lactation but had no predictive ability for $[THg]_{blood}$ late in lactation (Fig. 3c). Elephant seals are one of the longer-lactating phocids, and we sampled them at day 5 of an approximately 26-day lactation period (approximately one fifth of the way through lactation). Some phocids lactate for much shorter periods of time, with more intense maternal energy transfer, which results in higher proportion of neonatal mass gain per day (e.g., harp and hooded seals). For species that grow and wean faster than elephant seals, it is plausible that the strength of the relationship between [THg] in lanugo and blood weakens even faster than what we observed for elephant seals. Conversely, as we observed in

Steller sea lion pups, the strength of the relationship between $[THg]_{hair}$ and $[THg]_{blood}$ for species with slower growth rates that nurse for longer periods of time, such as otariids, may be more reliable for a longer period of time after birth. Together, these observations suggest that the ontogenetic phase of a developing animal is important to understand how Hg concentrations in hair relate to Hg concentrations in blood and potential toxicological risk.

Conclusion

We found intraspecific and interspecific variability in the strength of the relationship between [THg] in hair and blood likely because $[THg]_{hair}$ represents a "snapshot" of $[THg]_{blood}$ at the time the hair was formed (Wang et al. 2014), but [THg] in blood may change over time. The relationship between [THg] in hair and blood was affected by factors including age class, weaning status, growth, and the time difference between hair growth and sample collection. Hair [THg] was moderately to strongly predictive of $[THg]_{blood}$ in adults of three of the four species we sampled but poorly predictive for the species with the greatest fluctuation in body condition. Within species, we found that the ability of $[THg]_{hair}$ alone to predict current circulating $[THg]_{blood}$ was reduced in juvenile animals compared with adults with the exception of very young animals (14-day-old Steller sea lion and 5-day-old northern elephant seals pups), which is similar to trends observed between [THg] in down feathers and blood of juvenile birds (Ackerman et al. 2011). Additional factors may influence the relationship between [THg] in hair and blood that were not included in our analyses, such as the varying binding affinities for Hg in different blood compartments (Correa et al. 2014) and rapid changes in hematocrit that could result in significant changes in blood [THg], particularly in phocid seals (Castellini and Castellini 1989). Regardless, we show a number of cases, both for adult and prereproductive age classes, where $[THg]_{hair}$ was representative of circulating $[THg]_{blood}$, a tissue that can directly influence current toxicological risk. In conclusion, interpretation of [THg] in hair and blood in pinnipeds should incorporate an understanding of animal life history and molt dynamics to most accurately assess links between [THg] and foraging behavior as well as both current and past toxicological risk.

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