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Authors

Page, Annie
Hay, Clara
Marks, Wendy
et al.

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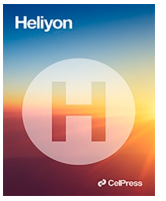

Research article

Trace element bioaccumulation, tissue distribution, and elimination in odontocetes stranded in Florida and Georgia, USA over a 15-year period (2007–2021)

Annie Page [a,*], Clara Hay [a,b], Wendy Marks [a], Baylin Bennett [c], Matthew O. Gribble [c], Wendy Noke Durden [d], Megan Stolen [e], Teresa Jablonski [d], Nadia Gordon [f], Trip Kolkmeyer [g], Mingshun Jiang [a], Nicole Pegg [a], Hunter Brown [a], Steve Burton [a]

[a] *Florida Atlantic University, Harbor Branch Oceanographic University, Fort Pierce, FL, USA*
[b] *United States Coast Guard Academy, New London, CT, USA*
[c] *University of Alabama at Birmingham, Birmingham, AL, USA*
[d] *Hubbs-SeaWorld Research Institute, Melbourne Beach, FL, USA*
[e] *Blue World Research Institute, Cocoa, FL, USA*
[f] *Florida Fish & Wildlife Conservation Commission, Fish & Wildlife Research Institute, Jacksonville, FL, USA*
[g] *Georgia Department of Natural Resources, Brunswick, GA, USA*

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ABSTRACT

Odontocetes obtain nutrients including essential elements through their diet and are exposed to heavy metal contaminants via ingestion of contaminated prey. We evaluated the prevalence, concentration, and tissue distribution of essential and non-essential trace elements, including heavy metal toxicants, in tissue (blubber, kidney, liver, skeletal muscle, skin) and fecal samples collected from 90 odontocetes, representing nine species, that stranded in Georgia and Florida, USA during 2007–2021. Samples were analyzed for concentrations of seven essential (cobalt, copper, iron, manganese, molybdenum, selenium, zinc) and five non-essential (arsenic, cadmium, lead, mercury, thallium) elemental analytes using inductively-coupled plasma mass spectrometry. Risso's dolphins (*Grampus griseus*) and short-finned pilot whales (*Globicephala macrorhynchus*) had the highest median concentrations of mercury, cadmium, and lead, while dwarf sperm whales (*Kogia sima*) had the lowest. Adult pygmy and dwarf sperm whales that stranded in 2019–2021 had higher concentrations of arsenic, copper, iron, lead, manganese, selenium, thallium, and zinc compared to those that stranded in 2010–2018, suggesting an increasing risk of exposure over time. The highest concentrations of many elements (e.g., cadmium, cobalt, copper, manganese, molybdenum, thallium, zinc) were in fecal samples, illustrating the usefulness of this non-invasively collected sample. Aside from fecal samples, hepatic tissues had the highest concentrations of iron, manganese, mercury, molybdenum, and selenium in most species; renal tissues had the highest concentrations of cadmium; skin had the highest concentrations of zinc; and copper, arsenic, and lead concentrations were primarily distributed among the liver and kidneys. Phylogenetic differences in patterns of trace element concentrations likely reflect species-specific differences in diet, trophic level, and feeding strategies, while heterogeneous distributions of elemental analytes among different organ types reflect differences in elemental biotransformation, elimination, and storage. This study illustrates the importance of monitoring toxic

* Corresponding author.
E-mail address: cpagekarjian@fau.edu (A. Page).

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contaminants in stranded odontocetes, which serve as important sentinels of environmental contamination, and whose health may be linked to human health.

1. Introduction

Various species of odontocetes ("toothed whales"; order: Cetacea; suborder: Odontoceti) inhabit the western North Atlantic Ocean bordering the southeastern United States and occasionally strand along southeastern beaches and other coastal areas. Two of the most common species to strand in the southeastern United States are pygmy (*Kogia breviceps*) and dwarf (*K. sima*) sperm whales [1–4]. These are small, cryptic odontocetes that inhabit temperate to tropical waters 400–3500 m deep along the continental shelf break and slope waters between Virginia and Florida [5–12]. Beaked whales (e.g., *Mesoplodon* spp.) strand less frequently and are thought to be sparsely distributed in tropical to warm-temperate waters along the shelf-edge and in deeper oceanic waters [12]. So-called 'blackfish', including pilot whales (*Globicephala* spp.), Risso's dolphins (*Grampus griseus*), melon-headed whales (*Peponocephala electra*), false killer whales (*Pseudorca crassidens*), and pygmy killer whales (*Feresa attenuata*), along with sperm whales (*Physeter macrocephalus*), inhabit deeper waters of the northwestern Atlantic Ocean and occasionally strand in the southeastern United States. As long-lived apex predators, these odontocete species are considered suitable environmental sentinels because they can potentially accumulate high quantities of contaminants, to which they are primarily exposed via ingestion of contaminated prey [13–17]. Despite their ecological importance, population status is unknown for many odontocete species in the northwestern Atlantic Ocean due to data deficiencies based on a lack of at-sea sightings and likely underreporting [12]. This has resulted in a current lack of federal protections for many species, even though population estimates are unsustainably small in many models (e.g., *Mesoplodon* spp.) [12]. Increased human activities in coastal areas, including increased industrial activities and increased inputs of contaminants into marine ecosystems, have accelerated threats to odontocete health and survival [3]. Thus, there is concern for the health of individual, free-ranging odontocetes as they are vulnerable to threats from human activities including fishing gear and/or marine debris ingestion and entanglement, vessel strikes, and exposure to pollutants including heavy metal toxicants such as arsenic, cadmium, lead, and mercury [3,18,19].

Odontocetes principally obtain nutrients through their diet, which consists primarily of teleost fishes and/or cephalopods (in variable proportions, depending on species). Ingestion is also the primary route of odontocetes' exposure to contaminants, including heavy metals [3,13,20,21]. Exposure to heavy metal contaminants constitutes a toxicological risk for odontocetes because it can result in oxidative stress, which can impair protein function, damage DNA, and disrupt membrane lipids [13–17,22], and has been linked to degenerative heart disease, immunodeficiency, and increased parasite infestations, among other disease risks [3,4,19,23–25]. Once exposed, odontocetes may accumulate heavy metals in their internal organs in a heterogeneous distribution among tissue types, since various elemental analytes may preferentially accumulate in certain organs (e.g., liver, kidney) depending on how they are metabolized and/or eliminated [3,15,17,20,21,26–29]. Because tissue concentrations of heavy metal contaminants also vary based on an individual animal's sex, age class, trophic level, and location, among other factors, it is important to first establish baseline values and then continue to monitor cetacean populations for exposure to these toxicants [3,4].

Previous studies have explored tissue concentrations and distributions of heavy metals and other trace elements in dolphins and toothed whales. While many studies have focused specifically on examining concentrations and molar ratios of mercury and selenium in odontocetes [30–37]; others have focused on heavy metals including mercury, cadmium, lead, and zinc [26–29,38–43]; and still others report results of extended analyses of many trace elements including essential and non-essential elements [3,4,17,44–48]. Data remain sparse, however, on how specific elements become distributed within a given animal's body, especially for many rarely encountered species, and how toxicant levels relate to animal signalment and other demographic factors. Up-to-date, baseline information on trace elements in free-ranging odontocete species is critically needed to establish species- and region-specific benchmark databases that enable comparisons and can contribute to our understanding of the role of trace element exposure in cetacean health and survival [3]. For this study, we hypothesized that elemental distribution within the tissues of wild odontocetes would vary depending on animal species, age class, sex, diet, and/or location. To address this hypothesis, the goal of this study was to evaluate the prevalence, concentrations, and tissue distributions of essential and non-essential trace elements, including heavy metal toxicants, in stranded odontocetes in the southeastern United States, and to interpret our results within the context of animal life history and stranding information.

2. Material and methods

2.1. Retrospective case series analysis

Stranding and necropsy reports were retrospectively examined for species, age class, sex, stranding year and region, body condition (e.g., thin [1], good [2], robust [3]), and tissues sampled from toothed whales that stranded alone or in cow-calf pairs along the southeastern coasts of Georgia and Florida, United States, during 2007–2021 [49]. Animals were either found alive and then euthanized, died upon stranding, or were found freshly dead (code 2); animal age classifications (fetus/neonate, juvenile, adult) were assigned based on species, total body length, and morphological characteristics. 'Calves' were classified as juveniles unless indicated to be neonates [3,50–54]. Neonates were excluded from this study. Species examined were pygmy sperm whales (*Kogia breviceps*), dwarf sperm whales (*Kogia sima*), Gervais' beaked whales (*Mesoplodon europaeus*), Risso's dolphins (*Grampus griseus*), short-finned pilot whales (*Globicephala macrorhynchus*), sperm whales (*Physeter macrocephalus*), melon-headed whales (*Peponocephala electra*), a

Blainville's beaked whale (*Mesoplodon densirostris*), and a false killer whale (*Pseudorca crassidens*).

2.2. Sample analysis

Skin, blubber, kidney, liver, skeletal muscle, and fecal samples collected at necropsy and stored at −80 °C were shipped overnight on dry ice to Michigan State University Veterinary Diagnostic Laboratory in Lansing, Michigan, USA, where they were analyzed for concentrations of 12 essential and non-essential elemental analytes (As, arsenic; Cd, cadmium; Co, cobalt; Cu, copper; Fe, iron; Pb, lead; Mn, manganese; Hg, mercury; Mo, molybdenum; Se, selenium; Tl, thallium; Zn, zinc) using inductively-coupled plasma mass spectrometry (ICP-MS, Agilent 7900 ICP-MS, Agilent Technologies, Santa Clara, CA, United States) in accordance with manufacturer's instructions. Samples were weighed and dry weight fractions were generated by drying wet samples at 75 °C overnight in a drying oven. Dried samples (~1 g) were weighed and digested with 1–2 mL (volume relative to weight per sample) of concentrated 69–70 % nitric acid (type J. T. Baker ACS reagent grade; Avantor Performance Materials, Center Valley, PA, United States) in 15 mL PFA digestion vessels (Savillex, Eden Prairie, MN, United States) in a 95 °C oven overnight. Prior to analysis, overnight digests were diluted 1:100 in Millipore Filter (Burlington, MA, United States) deionized water. Quality control (QC) for this process included the use of standard reference materials (SRMs) from the National Institute of Standards and Technology (NIST; Gaithersburg, MD, United States), including SRM 1577c Bovine Liver, NIST SRM 2976 Mussel, an in-house maintained QC-160 tissue spike control, and a digest blank. Results are presented in concentrations of parts per million dry weight (ppm dw).

2.3. Data curation and statistical analysis

Sample-specific limits of detection (LOD) were determined for each analyte (Supplemental Table S1). All compounds except arsenic, iron, selenium, and zinc had at least some samples below the LOD. For these analytes, the below detection limit (BDL) values were assigned a concentration of ½ the detection level to calculate summary statistics (mean, median, minimum, maximum, range) for each analyte. Detoxification of mercury and (to a lesser extent) cadmium is thought to occur in cetacean livers via a protective mechanism involving formation of a less toxic, selenium-bound complex, and the molar ratio of selenium to selected heavy metals is used to assess the potential for toxic health effects, wherein a molar excess (Hg:Se > 1) represents a greater risk for heavy metal toxicity [20,48,55]. Here, we used simple linear regression analyses to evaluate the strength and direction of the relationships between mercury and selenium, and cadmium and selenium, in liver samples from adults and juveniles of each species with $N > 3$. We also used simple linear regression to roughly evaluate the relationship between body condition and toxicant metabolism from lipid stores by comparing subjective body condition scores (1–3) to non-essential element concentrations in blubber samples from pygmy and dwarf sperm whales (the other species in this study were excluded from this analysis due to low sample sizes).

Shapiro-Wilk tests were used to evaluate the data for normality, and showed that overall, 74 % of variables had non-normal data distributions, and only 26 % of variables met the conditions for normality. Since most variables were not normally distributed and censored values were replaced with half the detection limit, we elected to use non-parametric statistical tests to analyze the data. Kruskal-Wallis rank sum tests for multiple independent samples, with a Bonferroni-corrected alpha of 0.0083 and post-hoc Dunn's tests with *P*-values adjusted by the Benjamini-Hochberg false discovery rate method, were used to compare the median concentrations of each elemental analyte between adults of each species with $N > 2$ (pygmy sperm whales, dwarf sperm whales, Risso's dolphins, and short-finned pilot whales); and between juveniles of each species with $N > 2$ (pygmy sperm whales, dwarf sperm whales, Gervais' beaked whales, and sperm whales). Kruskal-Wallis rank sum tests and post-hoc Dunn's tests were also used to compare the median concentrations of each elemental analyte between the six sample types (blubber, feces, kidney, liver, muscle, and skin) in adult pygmy sperm whales (Bonferroni-corrected $\alpha = 0.0033$), and between five sample types in adult dwarf sperm whales, Risso's dolphins, and short-finned pilot whales (fecal samples were not available for those species; Bonferroni-corrected $\alpha = 0.005$).

Since the majority (69.3 %) of samples were from pygmy and dwarf sperm whales, data from these two species were selected for more in-depth statistical analysis. For analysis of year stranded, cases were grouped into recent (e.g., 2019–2021) and less recent (e.g., 2009–2018) categories. Stranding locations were assigned to one of four bins, selected based on the stranding response areas of the Southeastern Marine Mammal Stranding Network members represented in this study (northeast, north-central, south-central, and south Florida). Left-censoring due to BDL samples was handled by Tobit regression where applicable; models with no BDL samples employed linear regression. Analyte concentrations were log-transformed for regression analysis. Models were stratified according to species and tissue type, and results are only shown for comparisons with $N \geq 5$ observations per stratum. Bootstrapping was used to produce bias-corrected and accelerated (BCa) confidence intervals [56] (Supplemental Table S2). Bonferroni correction was used to control the family-wise type I error rate at 0.05 by calculating the significance threshold $\alpha^* = 0.05/k$, where k is the number of models fitted ($k = 246$), to identify an appropriate confidence interval coverage ($1 - \alpha^*$) for the BCa. Tabulated results show 95 % BCa confidence intervals for all estimates. The estimated differences in mean log-chemicals were exponentiated to estimate the geometric mean ratios of chemicals, and BCa confidence interval bounds calculated on the log-chemical scale were exponentiated to generate the estimated confidence intervals for the geometric means. Data analyses were conducted using MedCalc statistical software (v.20.114; MedCalc Software, Ltd, Ostend, Belgium; https://www.medcalc.org; 2020), R Version (RStudio v.3.0), and Stata/IC (v.16.1, StataCorp LLC, College Station, Texas, USA; 2019).

3. Results

3.1. Animals, samples, and tissue-specific analyte baseline concentrations

Necropsies were conducted and tissue samples were collected from 90 individuals representing nine odontocete species that stranded in Georgia and Florida during 2007–2021 (Table 1). The body condition of these animals (with the exception of one whale) was assessed as either thin (26/90, 28.9 %), good (36/90, 40.0 %), or robust (27/90, 30.0 %) based on subjective visual evaluation by trained and experienced stranding response personnel [49]. From these 90 animals, 319 samples were analyzed, including 79 kidney, 77 liver, 62 skeletal muscle, 49 skin, 44 blubber, and 8 fecal samples. Summary statistics for concentrations of 12 elemental analytes in these tissue samples are shown in Table 2, including concentrations of seven essential elements (cobalt, copper, iron, manganese, molybdenum, selenium, zinc), and five non-essential elements (arsenic, cadmium, lead, mercury, thallium) that are considered heavy metal toxicants.

3.1.1. Elemental analyte concentrations – comparisons between species

Fig. 1 depicts the relative concentrations of the 12 elemental analytes quantified in each tissue type in increasing order and stratified by species and age class. Interspecific comparison of the median concentrations of elemental analytes in various tissue types sampled from adults and juveniles showed that mercury concentrations in liver and muscle samples from adult Risso's dolphins were significantly higher than mercury concentrations in liver ($P = 0.004$) and muscle ($P = 0.008$) samples from adult pygmy sperm whales, but not in blubber, kidney, or skin samples (all $P > 0.05$). Adult pygmy sperm whales also had lower kidney mercury concentrations than adult short-finned pilot whales ($P = 0.005$). Compared to adult dwarf sperm whales, adult Risso's dolphins had significantly higher concentrations of cadmium and mercury in blubber (both $P = 0.001$), liver (both $P = 0.002$), and muscle ($P < 0.001$, $P = 0.001$, respectively) samples; higher cadmium in kidney samples ($P = 0.002$); and higher mercury in skin samples ($P = 0.003$). Adult short-finned pilot whales had higher concentrations of mercury and cadmium than adult dwarf sperm whales, including higher mercury in kidney ($P = 0.003$), muscle ($P = 0.003$), and skin ($P < 0.001$) samples; and higher cadmium in kidney samples ($P = 0.004$). Liver samples from Risso's dolphins and short-finned pilot whales had significantly higher lead concentrations than those from dwarf sperm whales ($P = 0.008$, $P = 0.005$, respectively), and short-finned pilot whales had higher kidney arsenic concentrations ($P = 0.002$). Fewer differences were seen among juveniles, including statistically higher liver concentrations of cadmium ($P = 0.002$) and mercury ($P = 0.007$) in juvenile dwarf sperm whales compared to juvenile Gervais' beaked whales. All statistically significant, species-specific, and age-class-specific differences identified using Kruskal-Wallis rank sum tests with post-hoc Dunn's tests are shown in Supplemental Table S3.

3.1.2. Elemental analyte concentrations – comparisons between tissue types

The relative proportions of tissue-specific analyte concentrations for adult specimens of pygmy and dwarf sperm whales, Risso's dolphins, short-finned pilot whales, melon-headed whales, a Blainville's beaked whale, and a false killer whale are presented in Fig. 2. Results of Kruskal-Wallis rank sum tests for concentration differences between tissue types (Table 3, Supplemental Table S4) show that

Table 1
Demographic data for 90 odontocetes (representing nine species) that stranded on the coasts of Georgia and eastern Florida, USA during 2007–2021. Number and % of occurrences are shown for each category.

N (%)										
		Sex		Age Class		Stranding Location				
Species	Total	Male	Female	Juvenile	Adult	Georgia	North FL	North Central FL	South Central FL	South FL
Pygmy sperm whale *Kogia breviceps*	52 (58)	36 (69)	16 (31)	12 (23)	40 (77)	13 (25)	3 (6)	16 (31)	16 (31)	4 (8)
Dwarf sperm whale *Kogia sima*	16 (18)	10 (62)	6 (38)	4 (25)	12 (75)	3 (19)	1 (6)	9 (56)	3 (19)	0 (0)
Gervais' beaked whale *Mesoplodon europaeus*	5 (6)	2 (40)	3 (60)	4 (80)	1 (20)	0 (0)	1 (20)	1 (20)	3 (60)	0 (0)
Risso's dolphin *Grampus griseus*	4 (4)	2 (50)	2 (50)	1 (25)	3 (75)	0 (0)	0 (0)	4 (100)	0 (0)	0 (0)
Short-finned pilot whale *Globicephala macryrhynchus*	4 (4)	1 (25)	3 (75)	1 (25)	3 (75)	0 (0)	0 (0)	4 (100)	0 (0)	0 (0)
Sperm whale *Physeter macrocephalus*	4 (4)	4 (100)	0 (0)	4 (100)	0 (0)	0 (0)	0 (0)	2 (50)	1 (25)	1 (25)
Melon-headed whale *Peponocephala electra*	3 (3)	2 (67)	1 (33)	1 (33)	2 (67)	0 (0)	0 (0)	1 (33)	1 (33)	1 (33)
Blainville's beaked whale *Mesoplodon densirostris*	1 (1)	1 (100)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)
False killer whale *Pseudorca crassidens*	1 (1)	0 (0)	1 (100)	0 (0)	1 (100)	0 (0)	0 (0)	1 (100)	0 (0)	0 (0)
TOTAL (%)	**90 (100)**	**58 (64)**	**32 (36)**	**27 (29)**	**63 (71)**	**16 (18)**	**5 (5)**	**39 (44)**	**24 (27)**	**6 (7)**

in 40 adult pygmy sperm whales, fecal samples had the highest median concentrations of arsenic, cadmium, cobalt, copper, lead, manganese, molybdenum, thallium, and zinc. Liver samples had the highest concentrations of iron, mercury, and selenium, and the second-highest concentrations of copper, manganese, and molybdenum. Kidney samples had the second-highest concentrations of cadmium, cobalt, iron, lead, mercury, and thallium; muscle samples had the second-highest concentrations of arsenic; skin samples had the second-highest concentrations of zinc; and fecal samples had the second-highest concentrations of selenium (after liver samples). Blubber samples had the lowest median concentrations of all analytes except for lead, which was lowest in muscle samples.

In 12 adult dwarf sperm whales, kidney samples had the highest median concentrations of arsenic, cobalt, cadmium, mercury, and selenium, and the second-highest median concentrations of copper, iron, manganese, molybdenum, and zinc, compared to other sample types. Liver samples had the highest median concentrations of copper, iron, manganese, and molybdenum, and the second-highest median concentrations of cobalt, cadmium, and mercury. The highest median concentrations of zinc detected were in skin samples, and skin samples also had the second-highest median concentrations of selenium and lead. Blubber samples contained the highest median concentrations of lead, and the lowest concentrations of arsenic, cadmium, cobalt, copper, iron, manganese, mercury, molybdenum, selenium, and zinc. Median thallium concentrations were BDL for all sample types. Fecal samples were not available for comparison in this species.

Similar trends were observed in lower numbers of adult whales of other species, wherein iron, manganese, mercury, molybdenum, and selenium concentrations were highest in liver samples; the highest median concentrations of cadmium were found in kidney samples, followed by liver samples; copper concentrations were mostly distributed between the kidneys and liver; and the highest zinc concentrations were found in skin samples. Arsenic and lead were variably distributed among sample types, typically in low concentrations. In all samples, cobalt and thallium concentrations were either BDL or only present in trace amounts.

3.2. Modeling elemental concentrations and Kogiid demographics

Geometric mean ratios and 95 % BCa confidence intervals were calculated for essential and non-essential element distributions stratified by sex, age class, stranding year, and location in pygmy sperm whale tissues, with statistical significance based on 99.98 % BCa confidence intervals (Supplemental Table S5). Skeletal muscle samples collected from male pygmy sperm whales had 65 % lower cobalt and 43 % lower mercury concentrations than muscle samples from females. Compared to adults, juvenile pygmy sperm whales had significantly higher liver concentrations of arsenic (223 %), and lower liver concentrations of cadmium (91 %), mercury (76 %), and iron (34 %); lower kidney cadmium (96 %), mercury (77 %), and zinc (21 %); and lower muscle mercury (63 %) and iron (46 %). Pygmy sperm whales that stranded in Georgia had significantly higher liver concentrations of cobalt (77 %), molybdenum (77 %), manganese (71 %), and copper (44 %) compared to those that stranded along the north-central Florida coast, and higher kidney concentrations of lead (72 %) than those that stranded along the south-central Florida coast. Compared to those that stranded during 2019–2021, pygmy sperm whales that stranded during 2010–2018 had significantly lower liver concentrations of thallium (31 %) and lead (14 %); lower kidney concentrations of lead (14 %) and iron (6 %); lower skin concentrations of arsenic (13 %), selenium (10 %), and zinc (9 %); and lower selenium (24 %) and higher copper (7 %) concentrations in muscle samples (Fig. 3A).

Geometric mean ratios and 95 % BCa confidence intervals were also calculated for tissue samples collected from dwarf sperm whales, with statistical significance based on 99.98 % BCa confidence intervals (Supplemental Table S6). Compared to females, male dwarf sperm whales had significantly higher liver concentrations of copper (431 %) and higher blubber concentrations of molybdenum (294 %); and juveniles had higher blubber concentrations of selenium (189 %) and zinc (298 %) than adults. Compared to dwarf sperm whales that stranded during 2019–2021, those that stranded during 2009–2018 had significantly lower concentrations of arsenic in kidney (8 %) and muscle (13 %) samples, as well as lower concentrations of selenium (7 %) and higher concentrations of manganese in muscle (4 %) and blubber (88 %) samples (Fig. 3B).

3.3. Relationships between selenium, mercury, and cadmium

Molar ratios in liver concentrations of selenium and arsenic, cadmium, mercury, and lead were >1 for As:Se in a juvenile male Risso's dolphin; >1 for Cd:Se in four juvenile (one male, three females) Gervais' beaked whales, a juvenile male Risso's dolphin, and a juvenile female melon-headed whale; and >1 for Hg:Se in four juvenile (one male, three females) and one adult male Gervais' beaked whales, three adult (one male, two females) Risso's dolphins, three adult female short-finned pilot whales, one adult male and one juvenile female melon-headed whales, an adult male Blainville's beaked whale, and an adult female false killer whale. All other liver samples had molar ratios <1 for As:Se, Cd:Se, Hg:Se, and Pb:Se (Table 4). Simple linear regression analysis of the relationships between ratios of selenium, mercury, and cadmium concentrations in liver samples (Fig. 4, Supplemental Table S7) revealed statistically significant relationships in liver Hg:Se in pygmy sperm whales ($R^2 = 0.79$; $P < 0.001$), Gervais' beaked whales ($R^2 = 1.0$; $P < 0.001$), Risso's dolphins ($R^2 = 0.99$; $P = 0.006$), short-finned pilot whales ($R^2 = 1.0$; $P < 0.001$), and sperm whales ($R^2 = 0.99$; $P = 0.005$), and a weak, direct relationship in dwarf sperm whales ($R^2 = 0.07$; $P = 0.368$). Statistically significant relationships in liver Cd:Se ratios were identified in Gervais' beaked whales ($R^2 = 0.94$; $P = 0.007$), Risso's dolphins ($R^2 = 0.86$; $P = 0.074$), short-finned pilot whales ($R^2 = 0.199$; $P = 0.641$), sperm whales ($R^2 = 0.99$; $P = 0.004$), and pygmy ($R^2 = 0.35$; $P < 0.001$) and dwarf ($R^2 = 0.24$; $P = 0.079$) sperm whales. Linear regression analysis showed no statistically significant trends in the relationships between subjective body condition scores and elemental concentrations in blubber samples collected from pygmy and dwarf sperm whales (all were $R^2 < 0.30$; Supplemental Table S8).

Table 2
Mean ± standard deviation of concentrations of seven trace essential (cobalt, copper, iron, manganese, molybdenum, selenium, zinc) and five non-essential (arsenic, cadmium, lead, mercury, thallium) elements in six different tissue types collected from 90 odontocetes that stranded in coastal Georgia and eastern coastal Florida, USA during 2007–2021. Results are presented in concentrations of parts per million dry weight (ppm dw).

Tissue Type (*N*)	Mean ± SD (ppm dw)											
	Essential Elements								Non-Essential Elements			
	Cobalt	Copper	Iron	Manganese	Molybdenum	Selenium	Zinc	Arsenic	Cadmium	Lead	Mercury	Thallium
Pygmy sperm whale, *Kogia breviceps*, *N* = 52												
Adults (*N* = 40)												
Blubber (*15*)	0 ± 0	0.6 ± 1.0	44.3 ± 59.2	0.5 ± 0.9	0 ± 0	1.4 ± 1.0	7.1 ± 2.6	0.9 ± 0.4	0.2 ± 0.2	0 ± 0.1	1.1 ± 1.0	0 ± 0
Feces (*3*)	3.8 ± 2.1	718.0 ± 336.8	1083 ± 460.8	48.6 ± 16.4	1.6 ± 0.6	38.6 ± 8.7	1248 ± 610.5	11.2 ± 8.0	360.1 ± 432.3	8.7 ± 13.8	14.3 ± 2.6	0 ± 0
Kidney (*35*)	0.2 ± 0.1	8.9 ± 2.4	1202 ± 380.5	2.3 ± 0.7	0.2 ± 0.1	35.3 ± 14.2	84.3 ± 20.9	2.8 ± 1.4	108.5 ± 73.2	0.1 ± 0.2	19.4 ± 10.6	0 ± 0
Liver (*34*)	0.2 ± 0.1	17.5 ± 19.0	3300 ± 826.5	3.0 ± 2.5	0.6 ± 0.6	38.9 ± 20.5	48.8 ± 21.7	2.2 ± 1.6	21.6 ± 19.6	0.1 ± 0.1	41.6 ± 51.2	0 ± 0
Muscle (*24*)	0 ± 0	2.5 ± 0.9[bd]	1165 ± 263.4	0.6 ± 0.2	0 ± 0	5.1 ± 1.4	70.9 ± 36.5	4.0 ± 2.0	0.5 ± 0.3	0 ± 0	9.1 ± 3.2	0 ± 0
Skin (*19*)	0 ± 0	3.2 ± 2.0[bcd]	188.3 ± 227.1	1.5 ± 3.3	0.1 ± 0.1	23.6 ± 10.5	125.7 ± 51.3	1.9 ± 1.2	0.4 ± 0.2	0.1 ± 0.1	3.8 ± 1.9	0 ± 0
Juveniles (*N* = 12)												
Blubber (*2*)	0 ± 0	2.3 ± 3.0	19.1 ± 4.7	0.1 ± 0.1	0 ± 0	1.7 ± 0.7	4.6 ± 0.2	0.6 ± 0.1	0 ± 0	0 ± 0	0.4 ± 0.5	0 ± 0
Feces (*1*)	1.3	561.0	320.6	67.3	1.1	33.3	1622.7	18.7	95.1	0.4	9.3	0
Kidney (*10*)	0.2 ± 0.2	16.1 ± 20.5	1063 ± 1224	2.2 ± 1.1	0.2 ± 0.1	38.5 ± 19.0	67.9 ± 18.0	4.7 ± 2.8	23.2 ± 23.7	0.1 ± 0.1	6.3 ± 5.6	0 ± 0
Liver (*8*)	0.2 ± 0.1	112.8 ± 260.0	2306 ± 815.1	3.8 ± 3.0	0.4 ± 0.3	29.4 ± 10.3	50.1 ± 14.1	4.7 ± 3.3	4.5 ± 0.3	0.2 ± 0.4	6.5 ± 7.8	0 ± 0
Muscle (*6*)	0 ± 0	8.5 ± 12.5	655.2 ± 253.9	0.4 ± 0.2	0 ± 0	5.3 ± 2.8	53.5 ± 12.3	3.0 ± 1.3	0.1 ± 0	0.1 ± 0	3.7 ± 2.2	0 ± 0
Skin (*2*)	0 ± 0	2.9 ± 1.6	87.1 ± 53.4	0.5 ± 0	0 ± 0	46.2 ± 49.6	116.5 ± 89.0	6.2 ± 7.0	0.1 ± 0.1	0.1 ± 0.1	0.6 ± 0.1	0 ± 0
Dwarf sperm whale, *Kogia sima*, *N* = 16												
Adults (*N* = 12)												
Blubber (*10*)	0 ± 0	0.1 ± 0.1	21.4 ± 17.3	0.2 ± 0	0 ± 0	1.3 ± 0.9	1.0 ± 0.2	1.0 ± 0.2	0.1 ± 0.2	0.5 ± 0.4	0.5 ± 0.4	0 ± 0
Kidney (*10*)	0.2 ± 0.1	8.9 ± 2.9	1084 ± 298.9	2.9 ± 1.1	0.2 ± 0.1	49.3 ± 21.9	70.5 ± 20.5	3.3 ± 2.5	62.1 ± 45.3	0 ± 0	16.0 ± 11.1	0 ± 0
Liver (*10*)	0.1 ± 0.1	12.9 ± 14.1	2498 ± 961.3	3.3 ± 2.4	0.5 ± 0.5	29.5 ± 8.5	43.8 ± 28.2	1.1 ± 1.2	19.8 ± 28.9	0 ± 0	13.3 ± 14.9	0 ± 0
Muscle (*9*)	0 ± 0	2.4 ± 0.8	1052 ± 221.7	0.5 ± 0	0 ± 0	5.5 ± 1.7	55.1 ± 27.7	2.2 ± 1.5	0.4 ± 0.5	0 ± 0	7.3 ± 3.1	0 ± 0
Skin (*8*)	0 ± 0	3.7 ± 1.7	153 ± 92.0	0.9 ± 1.0	0.1 ± 0	36.6 ± 17.3	143.1 ± 68.0	1.2 ± 0.7	0.6 ± 0.6	0.1 ± 0.1	2.5 ± 0.8	0 ± 0
Juveniles (*N* = 4)												
Blubber (*2*)	0 ± 0	0.2 ± 0.1	45.3 ± 48.2	0.5 ± 0.5	0 ± 0	2.0 ± 0.3	12.9 ± 5.4	0.4 ± 0.3	0 ± 0	0.1 ± 0	0.1 ± 0	0 ± 0
Kidney (*3*)	0.1 ± 0	8.7 ± 1.1	1160 ± 283.0	3.4 ± 1.4	0.2 ± 0.1	26.9 ± 2.5	54.4 ± 2.9	2.8 ± 2.0	1.2 ± 2.0	0.2 ± 0.2	1.8 ± 1.7	0 ± 0
Liver (*4*)	0.1 ± 0.1	204.9 ± 246.7	2191 ± 617.3	4.5 ± 3.4	0.3 ± 0.2	23.8 ± 6.0	35.5 ± 17.5	1.4 ± 0.9	0.2 ± 0.3	0 ± 0	1.1 ± 0.9	0 ± 0
Muscle (*4*)	0 ± 0	3.9 ± 0.8	574.1 ± 102.5	0.6 ± 0.3	0 ± 0	5.6 ± 2.0	65.3 ± 20.0	3.8 ± 2.6	0.1 ± 0.2	0.1 ± 0.1	2.1 ± 2.2	0.1 ± 0.1
Skin (*2*)	0 ± 0	2.6 ± 0.6	61.2 ± 42.6	0.5 ± 0	0 ± 0	50.8 ± 8.3	265.0 ± 101.1	2.8 ± 1.4	0 ± 0	0.1 ± 0	0.4 ± 0.2	0 ± 0
Gervais' beaked whale, *Mesoplodon europaeus*, *N* = 5												
Adults (*N* = 1)												
Kidney (*1*)	0.1	6.0	1044	2.6	0.2	17.1	91.4	5.2	144.0	0.1	29.5	0
Liver (*1*)	0.1	36.2	1159	9.5	2.4	322.4	354.2	27.4	255.0	0.1	796.0	0.01
Juveniles (*N* = 4)												
Blubber (*1*)	0.01	0.1	13.0	0.2	0	1.2	3.0	0.9	0.1	0	3.0	0
Feces (*1*)	0.02	15.6	316.2	14.7	0.1	6.4	94.8	6.9	1.5	0.01	2.4	0
Kidney (*3*)	0.04	7.1	1526	2.2	0.3	19.5	100.6	1.5	71.6	0.04	43.3	0
Liver (*3*)	0.02	9.2	1697	10.6	1.5	37.4	95.9	4.2	13.6	0.04	98.9	0
Muscle (*3*)	0	2.0	1086	0.5	0.03	10.2	40.0	0.3	0.1	0.02	28.6	0
Skin (*2*)	0.1	1.7	115.7	0.5	0.1	22.9	967.7	1.6	0.1	0.01	8.1	0
Risso's dolphin, *Grampus griseus*, *N* = 4												
Adults (*N* = 3)												
Blubber (*3*)	0.1 ± 0.0	1.6 ± 1.4	156.0 ± 109.9	0.2 ± 0.2	0.04 ± 0.0	22.6 ± 12.2	30.6 ± 14.0	4.8 ± 5.9	6.6 ± 2.8	0.1 ± 0.1	31.3 ± 15.8	0 ± 0
Kidney (*3*)	0.1 ± 0.1	17.6 ± 3.8	872.8 ± 1.1	4.3 ± 1.1	0.2 ± 0.1	41.2 ± 17.3	127.5 ± 24.4	2.2 ± 0.9	295.8 ± 109.9	0.1 ± 0.1	57.6 ± 33.8	0.01 ± 0

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Table 2 (*continued*)

Tissue Type (*N*)	Mean ± SD (ppm dw)											
	Essential Elements								Non-Essential Elements			
	Cobalt	Copper	Iron	Manganese	Molybdenum	Selenium	Zinc	Arsenic	Cadmium	Lead	Mercury	Thallium
Liver (*3*)	0.04 ± 0.0	26.6 ± 16.6	2895 ± 471.0	6.2 ± 3.7	1.0 ± 0.8	327.1 ± 255.0	97.3 ± 34.9	3.6 ± 3.7	247.3 ± 114.3	0.2 ± 0.1	651.5 ± 584.6	0 ± 0
Muscle (*3*)	0.02 ± 0.0	4.0 ± 1.1	1219 ± 87.2	0.8 ± 0.4	0.01 ± 0.0	16.4 ± 8.3	52.8 ± 6.7	1.6 ± 0.7	5.2 ± 0.7	0.04 ± 0.0	40.8 ± 20.9	0 ± 0
Skin (*3*)	0.01 ± 0.0	3.1 ± 0.3	15.4 ± 3.6	0.5 ± 0.0	0.05 ± 0.0	150.1 ± 91.2	1240 ± 491.4	1.3 ± 0.4	0.7 ± 0.7	0.1 ± 0.0	13.4 ± 2.9	0 ± 0
Juveniles (*N* = 1)												
Blubber (*1*)	0.02	0.8	45.7	0.2	0.01	6.4	15.9	3.0	1.1	0.02	0.7	0
Kidney (*1*)	0.2	15.5	972.0	4.9	0.2	32.2	130.1	8.8	157.7	0.01	11.3	0.01
Liver (*1*)	0.1	24.2	2004	17.6	1.4	28.3	232.1	35.9	73.0	0.1	22.7	0
Muscle (*1*)	0.01	2.9	411.2	0.5	0.01	3.5	70.5	4.3	0.3	0.2	5.3	0
Skin (*1*)	0	4.5	6.5	0.5	0.01	303.1	902.5	4.0	0.1	0.1	4.4	0
Long-finned pilot whale, *Globicephala melas*[a], *N* = 4												
Adults (*N* = 3)												
Blubber (*3*)	0 ± 0	0.4 ± 0.1	28.9 ± 17.8	0.2 ± 0.2	0 ± 0	4.6 ± 1.3	17.2 ± 2.5	1.2 ± 0.1	0.5 ± 0.1	0 ± 0	5.3 ± 3.6	0 ± 0
Kidney (*3*)	0.1 ± 0.1	15.5 ± 4.7	883.8 ± 508.6	3.3 ± 0.4	0.1 ± 0	49.8 ± 28.4	108.4 ± 37.0	4.3 ± 1.9	175.5 ± 124.8	0 ± 0	60.7 ± 48.7	0 ± 0
Liver (*3*)	0 ± 0	13.2 ± 4.8	1959 ± 601.3	7.5 ± 3.4	0.7 ± 0.4	197.0 ± 261.0	132.3 ± 29.0	3.5 ± 2.1	64.8 ± 48.5	0.1 ± 0.1	431.1 ± 617.0	0 ± 0
Muscle (*3*)	0 ± 0	2.5 ± 0.8	984.2 ± 385.1	0.5 ± 0	0 ± 0	8.5 ± 4.7	79.2 ± 5.2	4.0 ± 0.7	0.7 ± 0.3	0 ± 0	27.6 ± 14.9	0 ± 0
Skin (*3*)	0 ± 0	4.5 ± 0.3	23.3 ± 10.2	0.5 ± 0	0 ± 0	183.6 ± 35.5	2427 ± 264.5	1.8 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	17.5 ± 2.8	0 ± 0
Juveniles (*N* = *1*)												
Blubber (*1*)	0	0.1	42.2	0.2	0	1.2	7.5	0.3	0.01	0	0.1	0
Kidney (*1*)	0.02	11.1	295.2	2.9	0.07	13.4	61.0	1.8	3.0	0.01	3.1	0
Liver (*1*)	0	14.9	1284	11.8	0.3	18.0	160.1	1.0	1.4	0.01	3.8	0
Muscle (*1*)	0	2.7	415.5	0.5	0.01	4.3	56.7	1.2	0.02	0.03	3.3	0
Skin (*1*)	0	5.2	53.5	0.5	0.05	192.0	2016	0.8	0.04	0.12	2.3	0
Sperm whale, *Physeter macrocephalus*, *N* = 4												
Juveniles (*N* = 4)												
Blubber (*3*)	0 ± 0	0.9 ± 0.7	62.1 ± 69.7	0.2 ± 0.1	0 ± 0	1.4 ± 0.8	20.1 ± 12.5	0.3 ± 0.1	0 ± 0	0 ± 0	0.2 ± 0.1	0 ± 0
Feces (*1*)	1.8	406.9	415.7	12.8	1.1	13.5	303.1	5.1	91.6	0.2	1.7	0
Kidney (*4*)	0.1 ± 0	16.3 ± 7.4	679.8 ± 374.3	2.1 ± 1.1	0.2 ± 0.1	16.1 ± 7.9	99.3 ± 21.4	3.3 ± 2.8	8.2 ± 15.7	0.2 ± 0.3	2.8 ± 2.3	0.2 ± 0.3
Liver (*4*)	0.1 ± 0.1	45.3 ± 32.9	2225 ± 1016	3.8 ± 2.5	0.5 ± 0.2	14.7 ± 17.3	98.8 ± 19.3	1.3 ± 1.1	2.7 ± 5.3	0.2 ± 0.2	17.5 ± 28.2	0.1 ± 0.2
Muscle (*3*)	0 ± 0	3.5 ± 0.3	568.2 ± 316.9	0.6 ± 0.2	0.1 ± 0.1	2.4 ± 0.7	153.1 ± 13.9	0.8 ± 0.3	0 ± 0	0 ± 0	1.5 ± 0.9	0 ± 0
Skin (*3*)	0 ± 0	8.5 ± 5.4	105.4 ± 146.6	0.5 ± 0	0.1 ± 0	32.6 ± 17.9	788.4 ± 500.2	1.2 ± 0.6	0.1 ± 0.1	0.2 ± 0.2	2.0 ± 0.7	0.2 ± 0.3
Melon-headed whale, *Peponocephala electra*, *N* = 3												
Adults (*N* = 2)												
Blubber (*1*)	0.01	0.2	13.7	0.2	0	1.8	10.9	0.4	0.2	0.01	2.5	0.01
Feces (*1*)	0.1	8.8	309.1	2.5	0.2	21.2	110.2	1.5	1.2	0.04	3.4	0
Kidney (*2*)	0.4 ± 0.4	10.0 ± 0.5	635.0 ± 37.7	2.8 ± 0.4	0.1 ± 0	31.1 ± 2.9	105.6 ± 13.0	1.2 ± 0.3	220.4 ± 1.8	0 ± 0	35.9 ± 0.7	0 ± 0
Liver (*1*)	0.02	6.8	2451	3.5	0.4	64.5	48.0	0.5	31.1	0.03	145.7	0
Muscle (*2*)	0 ± 0	3.4 ± 0	1116 ± 39.0	0.5 ± 0.1	0 ± 0	4.3 ± 2.2	69.4 ± 24.1	0.4 ± 0	0.6 ± 0.3	0.1 ± 0.1	19.1 ± 7.8	0 ± 0
Skin (*2*)	0.5 ± 0.8	1.6 ± 0.8	25.8 ± 16.9	0.5 ± 0	0.01 ± 0	90.2 ± 52.9	766.0 ± 637.9	0.5 ± 0.1	0.2 ± 0.1	0 ± 0	14.4 ± 9.1	0 ± 0
Juveniles (*N* = 1)												
Feces (*1*)	0.01	12.6	133.4	3.2	0.10	5.2	103.3	0.3	0.40	0.01	9.2	0
Kidney (*1*)	0.07	8.0	730.7	2.1	0.07	17.3	86.9	0.85	219.5	0.01	18.0	0
Liver (*1*)	0.05	10.6	3634.2	11.3	1.08	34.9	66.5	0.6	47.1	0.04	75.1	0
Muscle (*1*)	0.02	4.7	1065	0.5	0.02	1.7	97.2	0.32	0.6	0.04	15.6	0
Skin (*1*)	0	1.5	15.9	0.5	0.01	38.6	499.7	0.38	0.1	0.01	8.7	0
Blainville's beaked whale, *Mesoplodon densirostris*[a], *N* = 1												
Adults (*N* = 1)												
Blubber (*1*)	0.04	0.4	59.0	0.2	0.01	1.5	9.3	1.1	0.1	0.02	2.5	0.00

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Table 2 (*continued*)

Tissue Type (*N*)	Mean ± SD (ppm dw)											
	Essential Elements								Non-Essential Elements			
	Cobalt	Copper	Iron	Manganese	Molybdenum	Selenium	Zinc	Arsenic	Cadmium	Lead	Mercury	Thallium
Kidney (*1*)	0.05	9.1	1210	1.7	0.2	22.5	104.7	4.2	57.7	0.01	29.6	0.00
Liver (*1*)	0.08	23.1	1918	11.2	1.8	132.5	137.7	8.1	26.0	0.03	368.4	0.01
Muscle (*1*)	0.0	2.2	1641	0.5	0.01	1.9	43.5	2.0	0.1	0.06	7.0	0.00
Skin (*1*)	0.0	1.8	115.1	0.5	0.04	46.1	841.2	1.4	0.2	0.03	7.1	0.00
False killer whale, *Pseudorca crassidens*[a], *N* = 1												
Adults (*N* = 1)												
Blubber (*1*)	0.02	1.1	11.6	0.2	0	9.2	26.7	2.3	0.2	0	19.2	0
Kidney (*1*)	0.06	11.3	1274	3.0	0.2	262.1	79.6	0.6	37.0	0.04	538.6	0.01
Liver (*1*)	0.02	18.7	1732	10.4	1.3	2061	181.4	0.4	33.6	0.44	5337	0.02
Muscle (*1*)	0	3.2	1070	0.5	0.01	89.9	71.6	0.2	0.2	0.04	265.7	0
Skin (*1*)	0	3.5	14.4	0.5	0.02	167.0	1693	0.4	0	0.04	122.7	0

Abbreviations: SD, standard deviation.

[a] Fecal samples were not available for some species.

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Fig. 1. The relative concentrations of 12 elemental analytes (arsenic, cadmium, cobalt, copper, iron, lead, manganese, mercury, molybdenum, selenium, thallium, zinc) quantified in each of six sample types (blubber, feces, kidney, liver, muscle, skin) are shown in order of increasing concentrations, stratified by species and age class. Nine species of odontocetes are represented, including pygmy (*Kogia breviceps*) and dwarf (*K. sima*) sperm whales, Gervais' beaked whales (*Mesoplodon europaeus*), Risso's dolphins (*Grampus griseus*), short-finned pilot whales (*Globicephala macrorhynchus*), sperm whales (*Physeter macrocephalus*), melon-headed whales (*Peponocephala electra*), a Blainville's beaked whale (*Mesoplodon densirostris*), and a false killer whale (*Pseudorca crassidens*).

4. Discussion

4.1. Demographic patterns of elemental accumulation – species comparisons

Essential trace elements have biological roles in homeostatic processes and therefore tend to have much shorter half-lives than non-essential trace elements, which have no known biological function and accumulate in tissues over time [48,57]. A current lack of fundamental information on trace elements in certain odontocete species warrants efforts to collect baseline data and establish benchmark comparisons, especially since bioaccumulation and toxicological effects may be species-specific [3].

When we separated phylogenetic groups into age classes and compared median concentrations of heavy metals in specific tissue types between adult specimens of species with $N > 1$, we found some interesting trends. Of all tissue samples analyzed, the highest concentrations of mercury and cadmium were in liver, blubber, and muscle samples from Risso's dolphins, as well as the highest kidney cadmium and the highest liver lead concentrations observed. The highest mercury concentrations in kidney and skin samples, and highest arsenic in kidney samples, were from short-finned pilot whales. The lowest median concentrations of mercury and cadmium in liver, kidney, blubber, and muscle samples, the lowest skin mercury concentration, and the lowest liver lead concentration, were all from dwarf sperm whales. When these species-specific comparisons are expanded to include species with only $N = 1$ specimen, an adult female false killer whale that stranded in north central Florida had the highest mercury concentrations of all liver (5337 μg/g), kidney (539 μg/g), blubber (19 μg/g), muscle (266 μg/g), and skin (123 μg/g) samples analyzed, respectively. The single highest kidney cadmium concentration (421 μg/g) was found in an adult female Risso's dolphin, and the single highest liver cadmium concentration (255 μg/g) was in an adult male Gervais' beaked whale. These concentrations far exceed the toxic effect thresholds of mercury (>100–400 μg/g wet weight or 400–1600 μg/g dry weight) and cadmium (>20 μg/g wet weight or ~100 μg/g dry weight) reported to trigger cellular and physiological damages of target organs, such as hepatocellular damage and renal dysfunction [3,30,38,39,42,44].

Concentrations of trace elements spanned 1–3 orders of magnitude, with the greatest variability in copper, iron, mercury, selenium, and zinc concentrations, and the least variability in cobalt and molybdenum concentrations– both of which were primarily at or near detection limits. The observed differences in patterns of trace element concentrations that arise by phylogenetic grouping likely reflect species-specific differences in diet, trophic level, and feeding strategies [48]. The species represented in this study all occupy high and similar trophic levels, and consume a mixture of cephalopods and fishes, with some preying almost solely on squid (e.g., Kogiid whales, Mesoplodont whales, sperm whales), while others consume relatively greater proportions of small pelagic fishes (e.g., Risso's dolphins, pilot whales, false killer whales) and crustaceans (e.g., melon-headed whales) [11,52–54,58–61]. Delphinid populations that primarily consume fish tend to accumulate greater concentrations of mercury than populations in the same region with diets composed primarily of cephalopods [29,48,62,63]. Conversely, populations that consume mainly cephalopods tend to accumulate greater concentrations of cadmium than piscivorous populations [26,29]. Cephalopods are at a lower trophic level than fish and are naturally enriched in cadmium, arsenic, and chromium (not measured here), and thus deep-diving odontocetes such as sperm whales and beaked whales are generally exposed to higher concentrations of these elements through their cephalopod-rich diet [29,48,64–67].

4.2. Demographic patterns of elemental accumulation – Kogiid whales

When pygmy and dwarf sperm whale cases were stratified by age class, we found that, of the non-essential elements, cadmium and mercury were higher in adult liver and kidney samples, mercury was higher in adult muscle samples, and arsenic was lower in adult liver samples compared to juveniles. Of the essential elements, iron was higher in liver and muscle samples from adult pygmy sperm whales, and zinc was higher in kidney samples. In dwarf sperm whales, adults had higher blubber selenium and zinc than juveniles. These results demonstrate that certain elements, including the toxic heavy metals cadmium and mercury, accumulate significantly with aging in individual animals, and are consistent with previous findings reported for stranded cetaceans [29,41,48].

When we compared elemental analytes in adult pygmy and dwarf sperm whales that stranded in 2010–2018 to those that stranded in 2019–2021, we found statistically significant trends of increasing concentrations of arsenic, copper, iron, lead, manganese, selenium, thallium, and zinc over time. These trends were apparent in multiple tissue types (blubber, kidney, liver, muscle, skin), and therefore do not seem isolated to specific tissues. These results suggest that cetaceans have been increasingly exposed to both essential (copper, iron, manganese, selenium, zinc) and non-essential (arsenic, lead, thallium) elements, likely related to rapid human development of coastal ecosystems in Florida and Georgia over the last two decades. These anthropogenic activities can rapidly increase the influx of metals and metalloids entering the marine environment, which can bioaccumulate and biomagnify in marine top consumers including cetaceans, and can have dose-dependent detrimental health effects at toxic exposure levels [48,68,69].

We also observed differences based on geographic location, as Kogiid whales that stranded in Georgia had higher cobalt, copper, lead, molybdenum, and manganese levels than Kogiids that stranded in Florida. While cetacean stranding locations do not necessarily

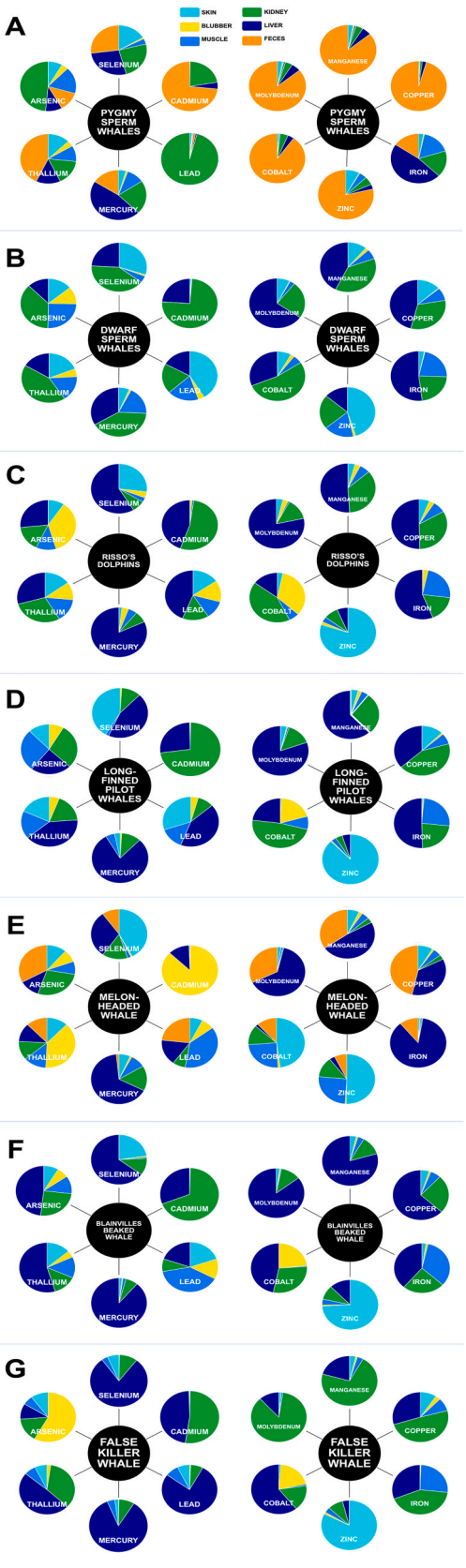

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Fig. 2. Relative proportions of tissue-specific concentrations of essential (cobalt [Co], copper [Cu], iron [Fe], manganese [Mn], molybdenum [Mo], selenium [Se], zinc [Zn]) and nonessential (arsenic [As], cadmium [Cd], lead [Pb], mercury [Hg], thallium [Tl]) elements identified in skin, blubber, skeletal muscle, kidney, liver, and fecal samples collected from stranded adult specimens of pygmy (*Kogia breviceps*) and dwarf (*K. sima*) sperm whales, Risso's dolphins (*Grampus griseus*), short-finned pilot whales (*Globicephala macrorhynchus*), melon-headed whales (*Peponocephala electra*), a Blainville's beaked whale (*Mesoplodon densirostris*), and a false killer whale (*Pseudorca crassidens*).

represent the location where they spent most their life, the regional differences in elemental concentrations identified here likely reflect variable exposure risk specific to certain geographic locations. For example, in 2012, Glynn County in coastal Georgia was determined to be the most biologically polluted coastline in the entire state [70], and in 2014 the Savannah River, which effluxes from the 100-mile Georgia coastline, was ranked as the 3rd most polluted waterway in the United States due to high levels of toxic discharges [71]. Mean total polychlorinated biphenyl (PCB) concentrations from dolphins biopsied in the Turtle/Brunswick River Estuary in south-central Georgia [72,73] exceeded those in dolphins sampled in other areas of the world including other inshore estuarine waters along the southeast coast of the United States, including east-central Florida and the Gulf of Mexico [4,74–78]. Although in our study these spatial trends were limited to pygmy sperm whales (a species with nearshore distribution), the impacts of water contamination are not limited to coastal waters. Humans inhabit coastal areas of the southeastern United States in dense populations and eat many of the same types of fishes and cephalopods commonly consumed by odontocetes. Thus, such results point to an important public health concern and warrant routine monitoring of heavy metals and other toxicants in these prey species and other fishes commonly consumed by humans to inform up-to-date guidelines for human consumption of marine fishes. These findings also illustrate the importance of monitoring toxic contaminants in stranded marine mammals, which serve as important sentinels of environmental contamination, and whose health may be linked to human health in specific geographic areas [4,24,79].

4.3. Tissue- and organ-specific patterns of elemental accumulation

Certain elements are known to accumulate in different tissues and organs of marine mammals [17]. Like previous studies that have reported wide variability in elemental concentrations between animals and tissue types, our results demonstrate heterogeneous distributions of elemental analytes among blubber, feces, kidney, liver, skeletal muscle, skin samples [3,17,21,26,28,46,48]. Such variations reflect differences in elemental biotransformation, elimination, and storage related to the specific molecular properties of each element and how they interact with cellular processes in different tissues [30]. The fecal samples evaluated in this study had relatively high concentrations of many elements (e.g., arsenic, cadmium, cobalt, copper, lead, manganese, molybdenum, thallium, zinc), highlighting the important role of hepatic metabolism, biotransformation, and excretion in maintaining cetacean homeostasis, and illustrating the usefulness of measuring analytes in fecal samples [80]. Aside from fecal samples, hepatic tissues had the highest concentrations of iron, manganese, mercury, molybdenum, and selenium in most species evaluated in our study; renal tissues had the highest concentrations of cadmium; skin had the highest concentration of zinc; and copper, arsenic, and lead were primarily distributed among the liver and kidneys. High hepatic concentrations of essential and non-essential elements are related to the important role of the liver in elemental biotransformation, detoxification, and storage. For example, the liver is the major site of iron storage and metabolism and is a key organ in the supply, storage, and excretion of copper [81,82]. The liver is also where mercury is methylated and forms complexes with selenium, and is ultimately stored [40,43,83]. Cadmium accumulation in kidney tissues of whales and dolphins is well-documented, including observation of solid granules of cadmium-calcium-phosphorus complexes in dolphin kidney tissues, suggesting there is a renal mechanism of cadmium sequestration, often without evidence of renal dysfunction [40,42,48,84,85]. Cetacean skin samples have been shown to be high in zinc in many previous studies, likely representative of the zinc requirements of actively proliferating and differentiating epidermal keratinocytes [85,86]. The skin of toothed whales represents a potential route for exposure to and absorption of dissolved environmental pollutants due to its particular structure composed of fragile superficial layers, where metallothioneins bind to heavy metals and contribute to zinc storage, and a dense sub-epithelial vascular system that carries absorbed molecules into systemic circulation [30,86].

4.4. Selenium aids in detoxification of mercury and cadmium

Mercury is one of the most toxic elements in marine systems, and it can bioaccumulate and biomagnify through marine food webs [87]. Cetaceans are exposed to mercury and other toxic metals mostly via ingestion of contaminated prey items, and tend to accumulate mercury in liver, muscle, and other tissues over time [29,44,88]. Selenium is an essential element that is a key component of many proteins and metalloenzymes, and is closely involved in detoxification of mercury and other heavy metals in cetaceans via formation of toxic metal-selenium complexes in the liver [31,32,34,45,48,89–91]. Here, analysis of these inter-elemental relationships showed strong positive correlations in liver mercury and cadmium concentrations in six odontocete species. This agrees with results from previous studies, and suggests a parallel accumulation of mercury, cadmium, and selenium in odontocetes when mercury and/or cadmium exceed(s) a certain concentration (e.g., 50 μg/g wet weight) [92,93]. Because of selenium's protective role in cetaceans exposed to toxic heavy metals, the molar ratio of mercury to selenium in liver samples is a useful parameter for assessing the potential for toxic health effects, wherein a molar excess (Hg:Se > 1) represents a greater risk for mercury toxicity [48]. Overall, there were 10 adults (four males, six females) and 12 juveniles (four males, eight females) with arsenic-, cadmium-, lead-, and/or mercury-to-selenium molar ratios >1, including 15 Hg:Se > 1, six Cd:Se > 1, and one As:Se > 1 (none had Pb:Se > 1). These results equate to a heavy metal toxicant molar excess in 16 % of all adults and 44 % of all juveniles evaluated. Previous reports of these trends

Table 3
Statistically significant, species-specific, and tissue-specific differences in elemental concentrations in blubber, kidney, liver, skeletal muscle, skin, and fecal samples collected from adult pygmy sperm whales (*Kogia breviceps*, *Kb, N* = 40), dwarf sperm whales (*Kogia sima*, *Ks, N* = 3), adult Risso's dolphins (*Grampus griseus*, *Gg, N* = 3), and long-finned pilot whales (*Globicephala melanogaster*, *Gm*, *N* = 3) that stranded in Georgia and eastern Florida during 2007–2021. Results generated using Kruskal-Wallis rank sum tests with post-hoc Dunn's tests and Bonferroni-corrected alpha values. Elemental analytes include seven essential (cobalt, copper, iron, manganese, molybdenum, selenium, zinc) and five non-essential (arsenic, cadmium, lead, mercury, thallium) elements.

Tissue Types Compared	Essential Elements							Non-Essential Elements				
	Cobalt	Copper	Iron	Manganese	Molybdenum	Selenium	Zinc	Arsenic	Cadmium	Mercury	Lead	Thallium
Blubber < kidney	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*
	Ks	*Ks*	*Ks*	*Ks*	*Ks*	*Ks*	*Ks*	*Gm*	*Ks*	*Ks*	*Ks*	
		Gm										
Blubber < liver	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*		
	Ks	*Ks*	*Ks*	*Ks*	*Ks*	*Ks*			*Ks*	*Ks*		
			Gm	*Gm*	*Gm*					*Gm*		
Blubber < muscle			*Kb*	*Kb*			*Kb*	*Kb*		*Kb*	*Ks*	
			Ks				*Ks*			*Ks*		
Blubber < skin		*Ks*		*Ks*	*Kb*	*Kb*	*Ks*				*Kb*	
					Ks	*Ks*	*Gg*				*Ks*	
						Gm	*Gm*					
Blubber < feces	*Kb*	*Kb*		*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*
Kidney > liver		*Kb*						*Ks*	*Kb*			
Kidney > muscle	*Kb*	*Kb*		*Kb*	*Kb*	*Kb*			*Kb*			*Kb*
	Ks	*Ks*			*Ks*	*Ks*			*Ks*			
Kidney > skin	*Kb*	*Kb*	*Kb*	*Kb*	*Kb*				*Kb*	*Kb*		
	Ks								*Ks*			
									Gg			
									Gm			
Liver > kidney			*Kb*									
Liver > muscle	*Kb*	*Kb*		*Kb*	*Kb*	*Kb*			*Kb*			
					Ks				*Ks*			
					Gg							
Liver > skin	*Kb*	*Kb*	*Ks*	*Kb*	*Kb*				*Kb*	*Kb*		
			Gg						*Gg*	*Gg*		
			Gm									
Liver > feces								*Kb*				
Muscle > liver								*Kb*				
								Ks				
Muscle > skin	*Gm*		*Kb*					*Kb*		*Kb*		
Skin > liver							*Kb*					
Skin > muscle						*Kb*	*Kb*					
						Ks						
Skin > feces							*Kb*					
Feces > kidney												*Kb*
Feces > liver												*Kb*
Feces > muscle	*Kb*	*Kb*		*Kb*	*Kb*	*Kb*			*Kb*		*Kb*	*Kb*
Feces > skin	*Kb*	*Kb*		*Kb*	*Kb*			*Kb*	*Kb*			*Kb*

Fig. 3. Geometric mean ratios and 95 % BCa confidence intervals for essential (cobalt, copper, iron, manganese, molybdenum, selenium, zinc) and nonessential (arsenic, cadmium, lead, mercury, thallium) element distributions stratified by sex, age class, stranding year, and location in **(A)** pygmy (*Kogia breviceps*) and **(B)** dwarf (*K. sima*) sperm whale tissues. Statistical significance was based on 99.98 % BCa confidence intervals.

have concluded that young cetaceans are unable to efficiently demethylate methylmercury, and that initiation of the demethylation process requires the total mercury concentration to reach a certain threshold value [13,34,36,94]. Another possible scenario is that maternal transfer of heavy metal contaminants results in juveniles starting life with relatively higher metals burdens, that they are then required to detoxify [33]. More recently, evidence from a study on short-finned pilot whales (*Globicephala macrorhynchus*) suggests that the selenium-mediated detoxification process is fully developed from an early age, and that the previously observed lack of demethylation products in tissues with total mercury concentrations below threshold values may be explained by the kinetic rates of the detoxification reactions, which are assumed to be slow based on slow distribution kinetics of dietary methylmercury between individual organs [37,95]. Molar ratios <1 in all other individuals indicate an excess of selenium, interpreted as adequate detoxification effects [47].

4.5. Limitations of the study

Although we consider this dataset to be an accurate representation of the stranded odontocetes in the studied region during the study period, sampling opportunities were limited to stranding events and therefore data sparsity was the primary limitation of this study. Limitations to the use of geometric mean ratios and 95 % BCa confidence intervals employed here include the fact that we used

Table 4
Molar ratios of liver concentrations of selenium (Se) and four heavy metal toxicants– arsenic (As), cadmium (Cd), mercury (Hg), and lead (Pb) in nine species of odontocetes that stranded along the southeastern United States during 2007–2021.

Species	As:Se	Cd:Se	Hg:Se	Pb:Se
Pygmy sperm whale, *Kogia breviceps*				
Adults, $N = 40$	0.08 ± 0.09 (0.56–7.41)	0.55 ± 0.38 (0.04–1.51)	0.83 ± 0.68 (0.11–2.03)	0.00 ± 0.01 (0.00–0.03)
Juveniles, $N = 12$	1.18 0.12 (0.03–0.36)	0.14 ± 0.14 (0.00–0.38)	0.21 ± 0.16 (0.05–0.53)	0.01 ± 0.02 (0.00–0.07)
Dwarf sperm whale, *Kogia sima*				
Adults, $N = 12$	0.04 ± 0.05 (0.01–0.17)	0.64 ± 0.70 (0.02–2.36)	0.48 ± 0.45 (0.03–1.14)	0.00 ± 0.00
Juveniles, $N = 4$	0.06 ± 0.03 (0.02–0.10)	0.01 ± 0.02 (0.00–0.03)	0.06 ± 0.07 (0.01–0.16)	0.00 ± 0.00
Gervais' beaked whale, *Mesoplodon europaeus*				
Adult, $N = 1$	0.08	0.79	2.47[a]	0.00
Juveniles, $N = 4$	0.58 ± 0.77 (0.01–1.71)	1.07 ± 1.02[a] (0.15–2.47)	1.97 ± 0.82[a] (1.14–2.87)	0.00 ± 0.00
Risso's dolphin, *Grampus griseus*				
Adults, $N = 3$	0.02 ± 0.01 (0.00–0.03)	0.98 ± 0.43 (0.55–1.41)	1.87 ± 0.27[a] (1.69–2.18)	0.00 ± 0.00
Juvenile, $N = 1$	1.27[a]	2.58[a]	0.80	0.00
Long-finned pilot whale, *Globicephalus melas*				
Adults, $N = 3$	0.04 ± 0.03 (0.01–0.06)	0.61 ± 0.40 (0.20–0.98)	2.02 ± 0.47[a] (1.47–2.30)	0.00 ± 0.00
Juvenile, $N = 1$	0.06	0.08	0.21	0.00
Sperm whale, *Physeter macrocephalus*				
Juveniles, $N = 4$	0.11 ± 0.03 (0.40–2.96)	0.08 ± 0.12 (0.00–0.26)	0.82 ± 0.48 (0.40–1.48)	0.17 ± 0.23 (0.01–0.50)
Melon-headed whale, *Peponocephala electra*				
Adult, $N = 1$	0.01	0.48	2.26[a]	0.00
Juvenile, $N = 1$	0.02	1.35[a]	2.15[a]	0.00
Blainville's beaked whale, *Mesoplodon densirostris*				
Adult, $N = 1$	0.06	0.20	2.78[a]	0.00
False killer whale, *Pseudorca crassidens*				
Adult, $N = 1$	0.00	0.02	2.59[a]	0.00

bootstrap with BCa confidence intervals to reduce the impact of parametric model assumptions for statistical inference, but the sampling variability of the bootstrap replicates may be limited by the number of necropsied animals. There are many combinations of species, tissue type, and demographic predictor variables (e.g., sex, age, geography) for which we did not have enough data (i.e., $N \geq 5$ observations per stratum) on which to present rigorous associations. Additionally, our Bonferroni corrections may be overly conservative. The observed biomarker levels across tissues represent not only levels of exposure, but also distribution and elimination processes that may be different between sick, stranded animals versus healthy wild animals. Robust associations across tissue types are more likely to reflect differences in chemical intake that may be toxicologically and nutritionally important for the health of odontocetes.

4.6. Conclusions

With this study, we evaluated the prevalence, concentrations, and tissue distributions of 12 essential and non-essential trace elements– including five heavy metal toxicants– in nine species of odontocetes that stranded in the southeastern United States, and interpreted our results within the context of animal life history and stranding information. Trace element concentrations varied widely among species, and we also identified variations within species depending on sex, age class, and other demographic factors. Phylogenetic differences in patterns of trace element concentrations likely reflect species-specific differences in diet, trophic level, and feeding strategies, while heterogeneous distributions of elemental analytes among different organ types reflect differences in elemental biotransformation, elimination, and storage. This study illustrates the importance of monitoring toxic contaminants in stranded odontocetes, which serve as important sentinels of environmental contamination, and whose health may be linked to human health. The results of this study provide important baseline data needed to further assess the pathophysiological mechanisms and ecotoxicological hazards associated with exposure to and accumulation of trace elements in tissues of free-ranging whales and dolphins.

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Data availability

Project data are publicly available online via the OSF data repository: https://osf.io/vu9pj/?view_only=09a64f3f7ab7404b89365fcb2539b256.

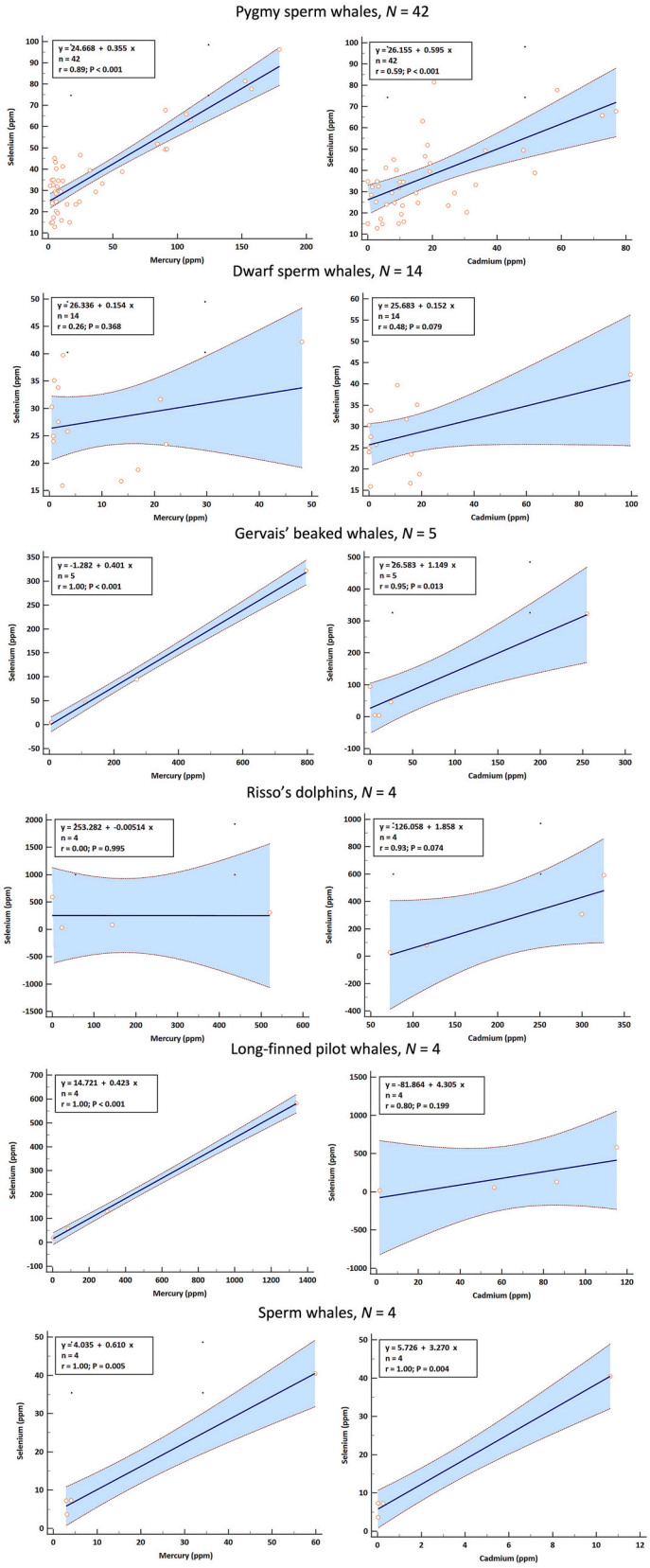

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Fig. 4. Simple linear regression analysis of the relationships between ratios of selenium, mercury, and cadmium concentrations in liver samples collected from stranded odontocetes revealed statistically significant relationships between liver mercury and selenium concentrations in pygmy sperm whales (*Kogia breviceps*), Gervais' beaked whales (*Mesoplodon europaeus*), Risso's dolphins (*Grampus griseus*), short-finned pilot whales (*Globicephala macrorhynchus*), and sperm whales (*Physeter macrocephalus*), and a weak, direct relationship in dwarf sperm whales (*Kogia sima*). Statistically significant relationships in liver cadmium and selenium concentrations were identified in Gervais' beaked whales, Risso's dolphins, short-finned pilot whales, sperm whales, and pygmy and dwarf sperm whales.

CRediT authorship contribution statement

Annie Page: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Clara Hay:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing – review & editing. **Wendy Marks:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing – review & editing. **Baylin Bennett:** Formal analysis, Methodology, Software, Visualization, Writing – review & editing. **Matthew O. Gribble:** Formal analysis, Methodology, Software, Visualization, Writing – review & editing. **Wendy Noke Durden:** Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Megan Stolen:** Data curation, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing – review & editing. **Teresa Jablonski:** Data curation, Investigation, Methodology, Project administration, Resources, Writing – review & editing. **Nadia Gordon:** Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Trip Kolkmeyer:** Data curation, Resources, Writing – review & editing. **Mingshun Jiang:** Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Nicole Pegg:** Data curation, Investigation, Methodology, Resources, Software, Validation, Writing – review & editing. **Steve Burton:** Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e25552.

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