The influence of depth on mercury levels in pelagic fishes and their prey

C. Anela Choy[a,1], Brian N. Popp[b], J. John Kaneko[c], and Jeffrey C. Drazen[a]

[a]Department of Oceanography, University of Hawaii, 1000 Pope Road, Honolulu, HI 96822; [b]Department of Geology and Geophysics, University of Hawaii, 1680 East-West Road, Honolulu, HI 96822; and [c]PacMar Inc., 3615 Harding Avenue, Suite 409, Honolulu, HI 96816

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Mercury distribution in the oceans is controlled by complex biogeochemical cycles, resulting in retention of trace amounts of this metal in plants and animals. Inter- and intra-specific variations in mercury levels of predatory pelagic fish have been previously linked to size, age, trophic position, physical and chemical environmental parameters, and location of capture; however, considerable variation remains unexplained. In this paper, we focus on differences in ecology, depth of occurrence, and total mercury levels in 9 species of commercially important pelagic fish (*Thunnus obesus*, *T. albacares*, *Katsuwonus pelamis*, *Xiphias gladius*, *Lampris guttatus*, *Coryphaena hippurus*, *Taractichthys steindachneri*, *Tetrapturus audax*, and *Lepidocybium flavobrunneum*) and in numerous representatives (fishes, squids, and crustaceans) of their lower trophic level prey sampled from the central North Pacific Ocean. Results indicate that total mercury levels of predatory pelagic fishes and their prey increase with median depth of occurrence in the water column and mimic concentrations of dissolved organic mercury in seawater. Stomach content analysis results from this study and others indicate a greater occurrence of higher-mercury containing deeper-water prey organisms in the diets of the deeper-ranging predators, *X. gladius*, *T. obesus*, and *L. guttatus*. While present in trace amounts, dissolved organic mercury increases with depth in the water column suggesting that the mesopelagic habitat is a major entry point for mercury into marine food webs. These data suggest that a major determinant of mercury levels in oceanic predators is their depth of forage.

depth of forage | marine pelagic predators | North Pacific Ocean | mercury bioaccumulation | mesopelagic zone

Mercury is a trace element distributed throughout the earth's atmosphere, biosphere, and geosphere. With numerous redox states, mercury is readily transformed by a suite of physical and biologically mediated reactions, which results in global biogeochemical cycling and trace retention in plants and animals. Mercury enters food webs following abiotic or biotic (i.e., bacterially mediated) methylation (1); after microbial uptake and subsequent consumer uptake, organic forms of mercury (primarily methylmercury) readily bind to proteins and bioaccumulate in higher trophic level organisms (2).

The presence of organic mercury in commercially important pelagic fishes (e.g., tunas, billfishes, and sharks) has long captured the interest of scientists, public health officials, and the general public (3, 4). Industrial activities have increased mercury emissions over past decades (5, 6), and growing awareness of the negative health impacts of mercury have forced many organizations (e.g., United States Environmental Protection Agency, Food and Drug Administration, and United Nations Environmental Program) to issue advisories and consider mercury emission controls. Thus, a comprehensive understanding of the environmental and ecological factors controlling mercury bioaccumulation in pelagic fishes is crucial for medical advisors and resource managers alike.

Variations in fish mercury levels have previously been linked to an assortment of synergistic factors such as location of capture (7, 8), trophic level (9, 10), environmental parameters (e.g., pH, temperature, algal concentrations) (11), and perhaps most commonly, size (12). Despite extensive measurements of mercury in both the environment and biota, it is still not known why, irrespective of size, some fish species have elevated mercury concentrations and others do not.

Biogeochemical studies detailing the movement of mercury between air, land, and ocean reservoirs have offered insight into where mercury may be distributed in the marine environment (13). In the Pacific Ocean specifically, vertical profiles show that methylated mercury species are usually below limits of detection in open ocean surface waters whereas subthermocline, low-oxygen deeper intermediate waters are sites for enhanced mercury methylation (14–17). Monomethylmercury (CH_3Hg) is the organic form of mercury that bioaccumulates in food webs and is toxic at elevated levels (1); therefore, if oxygen depletion is coupled with enhanced methylation rates in open ocean waters (16), it suggests that via the microbial loop (18), low oxygen deeper open ocean waters containing higher levels of bioavailable mercury will transfer elevated concentrations to animals both living at depth and predators foraging at depth. In support of this hypothesis, results of studies examining mercury levels in apex predatory seabirds suggest that the presence of mesopelagic prey in their diet may have contributed to elevated mercury levels (19, 20). Additionally, Monteiro et al. (21) found a positive mercury gradient with depth of occurrence in small epi- and mesopelagic fishes from the North Atlantic. However, these studies did not look concurrently at a diversity of predators and prey.

To better understand the mechanisms governing mercury bioaccumulation in open ocean animals, we examined mercury contents in predators and their lower trophic level prey in an ecological food web context. Using marine animals collected from waters surrounding Hawaii in the central North Pacific Ocean, we examined the hypothesis that animal mercury levels vary as a function of depth of occurrence in the water column. Ingestion of mercury from food has been confirmed as the dominant uptake pathway for fish, thus recording the integrated feeding behavior of the consumer (22, 23). Mercury levels were examined in 9 predatory pelagic fish species with distinct foraging behaviors and a representative collection of their prey items (fishes, cephalopods, and crustaceans comprising 56 taxa), inhabiting a large depth continuum.

Lastly, stomach content analysis of predators was used in the present study to corroborate satellite/recapture tagging studies that have demonstrated differences in vertical water column utilization among various pelagic fishes (24, 25), and augment diet data from published studies. By selecting predators with

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[1]To whom correspondence should be addressed. E-mail: cachoy@hawaii.edu.

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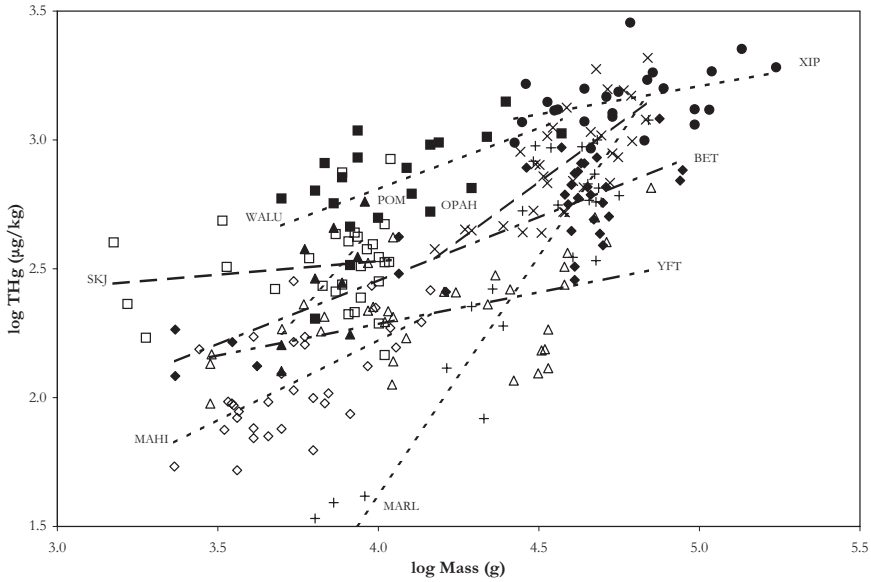

Fig. 1. Comparison of regressions of log-transformed THg concentrations (μg/kg) as a function of log-transformed body mass (g) for 9 predators. Broadbill Swordfish (*Xiphias gladius*), XIP (solid circles) ($n = 24$): THg = 0.22(mass) + 2.11, $r^2 = 0.18$; Bigeye Tuna (*Thunnus obesus*), BET (solid diamonds) ($n = 32$): THg = 0.49(mass) + 0.47, $r^2 = 0.71$; Moonfish or Opah (*Lampris guttatus*), OPAH (X's) ($n = 31$): THg = 0.92(mass) − 1.30, $r^2 = 0.56$; Skipjack Tuna (*Katsuwonus pelamis*), SKJ (open squares) ($n = 29$): THg = 0.11(mass) + 2.11, $r^2 = 0.02$; Yellowfin Tuna (*T. albacares*), YFT (open triangles) ($n = 34$): THg = 0.25(mass) + 1.30, $r^2 = 0.22$; Common Dolphinfish or Mahi-mahi (*Coryphaena hippurus*), MAHI (open diamonds) ($n = 33$): THg = 0.63(mass) − 0.28, $r^2 = 0.39$; Striped Marlin (*Tetrapturus audax*), MARL (crosses) ($n = 30$): THg = 1.85(mass) − 5.75, $r^2 = 0.84$; Sickle Pomfret (*Taractichthys steindachneri*), POM (solid triangles) ($n = 9$): THg = 1.42(mass) − 3.02, $r^2 = 0.40$; and Escolar (*Lepidocybium flavobrunneum*), WALU (solid squares) ($n = 20$): THg = 0.47(mass) + 0.91, $r^2 = 0.31$.

known foraging behaviors and prey with distinct vertical distributions it is likely that trophic transfers of mercury will be more clearly observed. The present approach is comprehensive in its coupling of analyses in predators and prey concurrently and provides information on food web dynamics and the factors governing mercury distributions in oceanic top predators.

Results and Discussion

Predators were designated as being either "shallow-ranging" (i.e., swimming/foraging generally above the thermocline) {*Coryphaena hippurus* [0–50 m (26)], *Thunnus albacares* [0–100 m (27)], *Tetrapturus audax* [0–100 m (28, 29)]; *Katsuwonus pelamis* [0–300 m (30, 31)]} or "deep-ranging" (i.e., with the ability to swim/forage below the thermocline) {*Taractichthys steindachneri* [300–500+ m (32, 33)], *T. obesus* [0–800 m (24, 34)], *Lampris guttatus* [25–700 m (25)], *Lepidocybium flavobrunneum* [200–885 m (35, 36)], *Xiphias gladius* [0–1,000 m (37)]} based on tagging data from Hawaiian waters. Using literature-derived depth distributions (see Table S1 for complete details), prey organisms were placed into 1 of 5 ecological depth categories created with respect to physical and ecological factors most likely to influence mercury content of the organisms (16, 17), namely day-time depth of occurrence. Briefly, "epipelagic" prey remain within the upper 200 m of the water column, while "upper-mesopelagic" and "lower-mesopelagic" prey are separated into diel vertical migrators and nonmigrators, where prey have median day-time depths between 200–600 m and 600–1,000 m, respectively.

Predator mercury concentrations varied widely (Fig. 1). Results from a generalized linear model (GLM) found that location (latitude and longitude as continuous variables) and sex did not have a significant effect on mercury concentrations but species and size did ($P < 0.05$). Fish size was designated a continuous variable within the GLM, while sex and species were categorical variables and fixed factors. The slopes of the mercury-size relationship were all positive, indicating that THg (total mercury, which includes all organic and inorganic species) concentrations increase with mass (Fig. 1) but the slopes varied as indicated by the significant interaction term between species and size ($P < 0.05$). All other interaction terms were not significant. Fish lengths were converted to ages (years) using published von Bertalanffy growth curves from the central North Pacific Ocean. Linear regressions examining the relationship between age and mercury concentration were significantly positive ($P < 0.05$) for 5 predators (age and growth not available for *L. guttatus*, *T. steindachneri*, *L. flavobruneum*, and *T. audax*). Age explained more variance in mercury than size. Inter- and intra-specific mercury variation has been attributed to size or age in numerous marine and freshwater studies (7, 10, 38, 39). The present results confirm these trends.

Mean THg concentrations for the 6 predator species in this study are similar to values previously reported for fishes from the central North Pacific Ocean (5, 40). More importantly, the relative rankings of THg concentrations by species in this study are in agreement with previous work (40).

Although size and age were important determinants of mercury concentrations considerable interspecific variation in mercury concentrations remained (Fig. 1). Depth was not included in the GLM because each species was represented by a single median depth and the variables were redundant. By regressing predator median depth of occurrence with size standardized mercury concentration we explained 76% of the residual variation ($P < 0.05$) (Fig. 2), showing a clear trend of increasing predator mercury concentrations with increasing median depth of occurrence. Conclusions of this statistical analysis are exemplified by the shallow-dwelling species *T. albacares* and *T. audax*, (yellowfin tuna and striped marlin, respectively), which are bigger and lower in mercury contents than the deeper-dwelling species *T. steindachneri* and *L. flavobrunneum* (sickle pomfret and escolar, respectively). We clearly show that the depth at which these predators forage directly influences their mercury concentrations.

Log-transformed mean THg concentrations of prey organisms varied significantly with prey median day-time depths (i.e., the

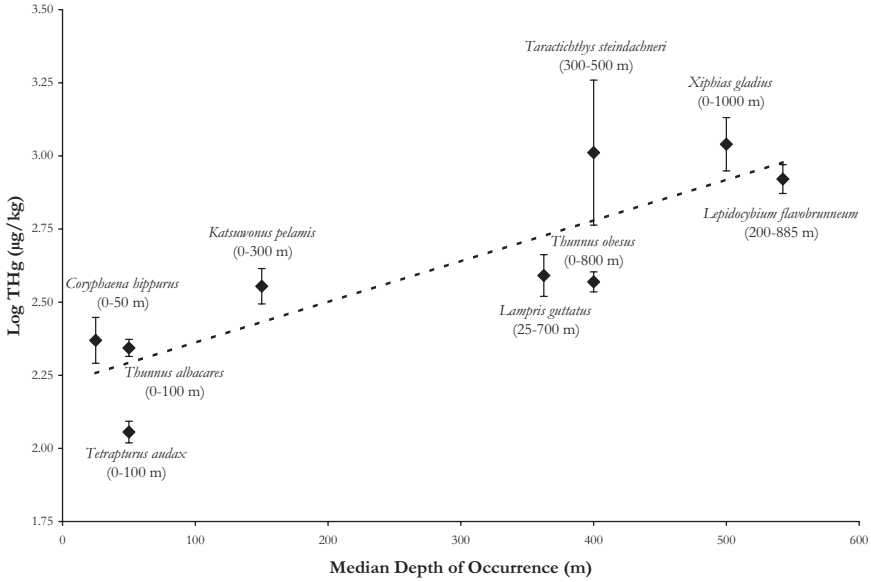

Fig. 2. Log-transformed mean THg concentrations (μg/kg) at the mean log(mass) of 4.24 or approximately 17.4 kg plotted as a function of median depth of occurrence for 9 species of pelagic fishes. Species names are given along with their depth ranges and standard error bars are shown. The overall regression of THg concentrations as a function of median depth of occurrence is significantly positive [Log THg = 0.0014(median depth of occurrence) + 2.2217; $P < 0.05$, $r^2 = 0.76$].

depth at which an animal spends the majority of its' time) as determined by ecological depth categories; the epipelagic prey group had significantly lower mean THg concentrations than all 4 of the remaining deeper-dwelling prey groups (ANOVA, $P < 0.05$). In addition, log-transformed THg concentrations and median day-time depths of prey organisms in this study were significantly positively correlated ($P < 0.05$, $r^2 = 0.34$) (Fig. 3). This general trend of increasing THg concentrations with increasing depth of occurrence in the prey suggests that the depth-related trend for the predators results from deeper-ranging species having access to deeper-living prey organisms with greater mercury concentrations.

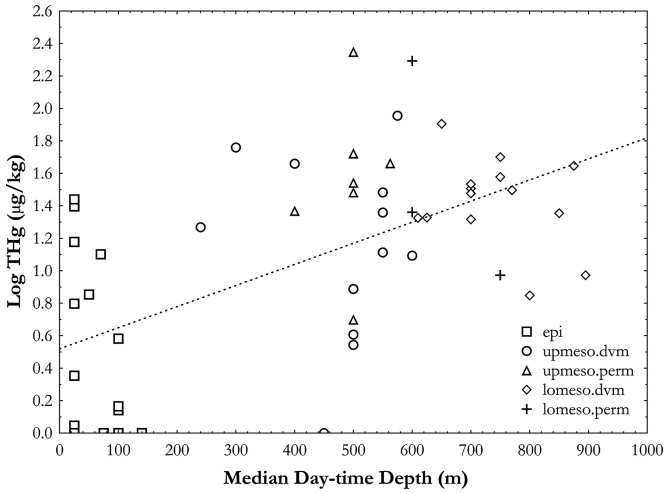

Fig. 3. Graphical relationship between log-transformed mean THg values (μg/kg) and median day-time depth (m) for all prey organisms per ecological depth category (epi = epipelagic prey, lomeso.dvm = lower-mesopelagic migrants, lomeso.perm = lower-mesopelagic nonmigrants, upmeso.dvm = upper-mesopelagic migrants, upmeso.perm = upper-mesopelagic nonmigrants). Equation for global regression line is Log(THg) = 0.0013(median day-time depth) + 0.5191, $P < 0.05$, $r^2 = 0.34$.

Relative to their shallow-water counterparts, the diets of the deep-ranging predators consisted of a greater numeric and gravimetric occurrence of mesopelagic prey items with day-time depths >200 m (Fig. 4). Differences in the relative importance of epi- and mesopelagic prey groups between shallow and deep-ranging predators are in agreement with conclusions from past diet studies (41–45) and evidence from tagging studies showing separation in vertical habitat utilization (24, 25, 27, 29, 31, 34, 35, 37), which are in turn explained by species-specific physiological capabilities. For example, it is well known that vascular countercurrent heat exchangers in scombrids allow tunas to access deeper colder waters while maintaining a body temperature above ambient levels (46). *K. pelamis* is the 1 exception; a shallow-ranging predator with a referenced depth range of 0–300 m, individuals from this study ingested a relatively high number of lower-mesopelagic prey items, almost all of which were the mesopelagic squid *Sthenoteuthis oualaniensis*. This squid has been found in epipelagic waters at night (47, 48) and it is likely that *K. pelamis* feeds on this and other deep-migrating cephalopods at night. Relative to similar-sized specimens of other shallow-ranging species (*C. hippurus* and *T. albacares*) in this study *K. pelamis* did display elevated mean mercury concentrations (Fig. 1).

Ultimately, because a predator obtains its' mercury from food, evidence that deeper-dwelling prey organisms have elevated mercury concentrations means that vertical differences in prey selection accumulated over the lifetime of a predator are crucial to mercury burdens.

In the pelagic realm, an understanding of the environments where bacterial communities convert inorganic mercury to bioavailable methylmercury is critical to tracing subsequent food web movement and accumulation patterns. The present data show that upper and lower-mesopelagic prey organisms whose day-time depths coincided with depleted oxygen waters [~600–1,000 m in the central North Pacific Ocean (49)] had elevated mercury concentrations relative to epipelagic prey organisms (Fig. 3). These results provide preliminary evidence to confirm biogeochemical studies hypothesizing enhanced mercury methylation with depth in the open ocean (14–17). Vertical profiles

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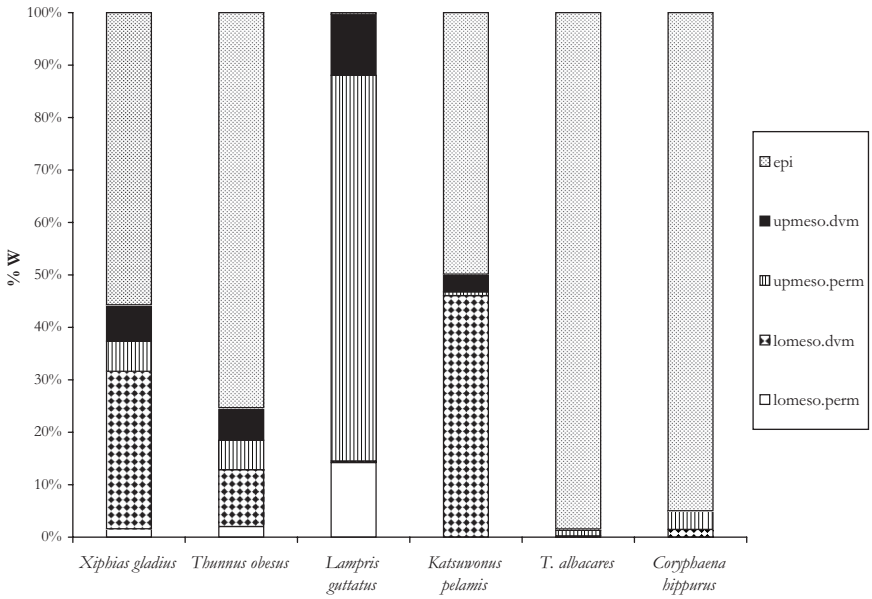

Fig. 4. Predatory diet composition based on identifiable prey items according to ecological depth groupings (epi, epipelagic; up.dvm, upper mesopelagic migrators; up.perm, upper mesopelagic nonmigrators; lo.dvm, lower mesopelagic migrators; lo.perm, lower mesopelagic migrators) (see *Results and Discussion* section of text for details). Diet is expressed as a function of the total gravimetric contribution of the prey (%W).

from the North Pacific show elevated levels of total-methylmercury (i.e., the sum of monomethylmercury and dimethylmercury) in intermediate, deeper open ocean waters, suggesting that particulate organic carbon transport and remineralization are linked to the production of organic mercury at depth (50). Similar data from open waters of the Mediterranean Sea link maximal total-methylmercury concentrations with depths of greatest oxygen consumption (51). Future work that is able to distinguish between bioavailable monomethylmercury and nonbioavailable dimethylmercury species with depth would provide further confirmation for our hypothesis.

Conclusions

After considering variability in age and size, increasing predatory mercury concentrations were clearly explained by increasing depth of occurrence. Prey mercury levels were also significantly positively correlated with day-time depth of occurrence. In agreement with established dietary studies, stomach content results from this study showed a greater relative contribution of deeper-dwelling, higher mercury containing prey in deeper-ranging predators compared to shallow-ranging. Thus, vertical differences in foraging behaviors over the lifetime of a pelagic predator are likely to be directly responsible for total mercury burdens.

Differences in vertical habitat utilization by co-occurring species of commercially important pelagic fishes have formed the basis of numerous management questions (52). Understanding the trophic ecology of these economically exploited predators is crucial if they are to be efficiently managed for the sustainable use of future generations. Results from this study may directly benefit fishery managers using ecosystem-based management strategies by offering predictive value to defining large-scale trophic links and the flow of organic matter and trace elements within marine pelagic ecosystems. Results of this study also provide the fish-consuming public with information about the mercury contents of popularly eaten marine fish species. Finally, our data support recent conclusions that the main source of methylmercury in the open ocean is from the deep water column (50, 51) and not export from coastal regions (13) or the euphotic zone (53).

Materials and Methods

Sampling Methods. Prey samples were collected using mid-water trawls (0–650 m) in April through May of 2007 and 2008 at Cross Seamount near Hawaii (located ≈295 km south of Oahu at 18°45′ N, 158°15′ W). Mixed zooplankton samples (1–2 mm size) were collected from Station ALOHA (22.5° N, 158° W) in the central North Pacific Ocean with a 1-m^2 plankton net with 202-μm mesh using oblique tows from the surface to 175 m depth (54).

Predator stomach and tissue samples were primarily collected by trained fishery observers of NOAA's Hawaii Observer Program, working on commercial vessels operating in the central North Pacific Ocean. Observers recorded species, forklength, sex, and date. Predator samples were also collected onshore from recreational boat captains in a similar manner. *L. guttatus* specimens captured in the central North Pacific Ocean were sampled from a local seafood wholesaler. *T. audax*, *T. steindachneri*, and *L. flavobruneum* were sampled directly from the Honolulu Fish Auction, as in Kaneko and Ralston (40). Catch locations of predators were all within a section of the central North Pacific Ocean bounded by 35 and 10° N latitude, and 190 and 215° W longitude.

Stomach Content Analysis. Using standard stomach content analysis protocols (55) predator stomachs were analyzed for diet composition relative to prey vertical habitat. The percent contribution of the total weight of the prey for each ecological prey category was summarized for each predator (% W).

Analytical Methods. Predator and prey white muscle tissue samples were analyzed for total mercury (THg) using atomic absorption spectrophotometry (Direct Mercury Analyzer, Milestone) (56, 57). Drying temperatures and decomposition times were chosen based on Milestone's recommendations for fish tissue. Methylmercury on average comprises more than 95% of all mercury present in fish tissue (58), thus THg measurements in this study serve as a viable proxy for methylmercury levels. All concentrations are reported on a wet-weight basis.

Primary and daily calibration of the instrument was performed using prepared aqueous standards over both the low (0–20 ng Hg) and high (20–1,000 ng Hg) working ranges. Method blanks and standard reference materials (SRM) (TORT-2 (0.27 ± 0.06 mg/kg Hg) for the low working range; ERM-CE464 (5.24 ± 0.10 mg/kg Hg) for the high working range) were analyzed at the end of every 10 samples to assess instrument accuracy and assure calibration curve stability. Prepared aqueous mercury standards were also used during analysis to verify the working calibration curve. To assess precision, 2 replicate analyses were performed at the beginning of every 10 samples; if the relative percent difference was within 5%, THg values for the remaining samples were used. To prevent carryover, blanks were analyzed between samples expected to have high THg concentrations.

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