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ECOLOGICAL FACTORS REGULATING MERCURY CONTAMINATION OF FISH FROM CADDO LAKE, TEXAS, USA

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Abstract—Most studies examining the influence of ecological characteristics of fish on Hg concentration in fish tissues have focused on a few variables and been conducted in northern ecosystems. We examined how total length (TL), age, food-web position (estimated using $\delta^{13}C$ and $\delta^{15}N$), and habitat were related to total Hg concentrations in 10 species of fish from Caddo Lake, a subtropical reservoir located on the border of Texas and Louisiana, USA. We observed biomagnification in the Caddo Lake fish assemblage, and the enrichment factors (the slope of the relationship between $\delta^{15}N$ and total Hg concentration) in the two habitats were 0.19 and 0.24, similar to those found in other studies. Although trophic position was the best predictor of total Hg concentration between species, age and TL were the best predictors of total Hg concentration within species. Unlike studies conducted in deep lakes, $\delta^{13}C$ values of fish tissue, a measure of the extent to which fish feed in food webs based on pelagic or littoral primary production, was not a good predictor of total Hg concentration in Caddo Lake fish. Total Hg concentrations in fish were elevated in forested-wetland habitats relative to open-water habitats. Data collected in the present study indicate that more Hg likely was available for incorporation into the base of the food web in the forested-wetland habitat than in the open-water habitat. Our results help to clarify the relationship between ecological characteristics of fish and Hg concentration in fish tissue and can be used by researchers as well as public and environmental health officials when designing Hg monitoring studies.

Keywords—Mercury Stable isotopes Fish Biomagnification Shallow reservoir

INTRODUCTION

Mercury is a teratogenic neurotoxin that accumulates in food webs, and Hg levels have increased in the environment because of anthropogenic activities, including the burning of coal for electricity generation, metal production, and waste incineration [1]. These anthropogenic activities emit several forms of Hg (elemental Hg, ionic Hg, and particulate Hg) to the atmosphere that are transported variable distances before being deposited onto the earth's surface [1]. In aquatic ecosystems, bacteria convert ionic Hg to bioaccumulative methylmercury (MeHg) [1]. Organisms at the base of the food web, such as phytoplankton and periphyton, concentrate MeHg directly from the water [1,2], whereas fish are exposed primarily to MeHg through their diets [1].

Because Hg-contaminated fish are the primary source of Hg to humans and wildlife, considerable interest exists to determine the factors that influence the concentration of Hg in fish tissues. Recognition is growing that ecological characteristics of fish affect their level of Hg contamination [3]. Mercury concentrations in fish are positively correlated with fish size, age, and trophic position [4–6]. Fish that feed in food webs based on phytoplankton primary production often are more contaminated with Hg compared to fish that feed in food webs based on periphyton primary production [7–9]. Finally, fish that live in habitats with high MeHg availability have elevated concentrations of Hg in their tissues [3,10]. Most studies that have examined the influence of ecological characteristics of fish on Hg concentrations in fish tissues have focused on a few variables [7], and it is not well understood which ecological characteristics are the best predictors of Hg concentration in fish.

Much of our understanding about the factors regulating Hg concentrations in fish is a result of studies conducted in northern ecosystems [5,7,11], whereas relatively few studies of Hg contamination in fish from subtropical regions, such as the southeastern United States, have been reported [12]. The southeastern United States has high rates of Hg deposition (Mercury Deposition Network, http://nadp.sws.uiuc.edu/mdn/), numerous coal-burning power plants that emit large amounts of Hg [13], and extensive wetland habitats [14], which may exacerbate the Hg contamination problem by efficiently converting inorganic Hg to MeHg [10,11]. All states in the region have issued fish consumption advisories because of high concentrations of Hg in fish (U.S. Environmental Protection Agency [EPA] National Listing of Fish Advisories, http://epa.gov/waterscience/fish/advisories/index.html).

We surveyed Hg contamination in several species of fish from Caddo Lake, a subtropical reservoir located on the border of Texas and Louisiana, USA, and determined the relative importance of factors influencing Hg concentrations in these species. Specifically, we examined how fish total length (TL), age, food-web position (measured using $\delta^{15}N$ and $\delta^{13}C$), and habitat were related to Hg concentrations in 10 species of fish from Caddo Lake. Caddo Lake is used by both recreational and subsistence anglers [15,16], and it also is home to rare and threatened wildlife species (Caddo Lake Ramsar Designation, http://www.caddolakeinstitute.us/ramsar.html). As a secondary objective, we compared Hg concentrations of fish

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collected in the present study to U.S. EPA benchmarks to assess the potential impact of consuming Hg-contaminated fish from Caddo Lake on human and wildlife health.

MATERIALS AND METHODS

Study site

Caddo Lake is a large (107 km^2), shallow (most areas <3 m) reservoir, with a mean depth of 1.4 m [17,18]. Water-chemistry data for Caddo Lake is available from the Northeast Texas Municipal Water District (Cypress Creek Basin Summary Report, http://www.netmwd.com/reports/reports.html). The western portion of the lake ($\sim$40 km^2, mostly in Texas) is composed primarily of a forested wetland (hereafter referred to as wetland) dominated by bald cypress (*Taxodium distichum*) and other submerged and emergent aquatic vegetation [18,19]. The eastern portion of Caddo Lake (mostly in Louisiana) is primarily open-water habitat, though submerged vegetation can be extensive in summer months. The most probable source of Hg loading into Caddo Lake is atmospheric deposition [20]. The primary anthropogenic sources of Hg in the region are coal-burning power plants (U.S. EPA, 2006 Toxic Release Inventory Program, http://www.epa.gov/tri/). Fish consumption advisories have been issued for largemouth bass (*Micropterus salmoides*) and freshwater drum (*Aplodinotus grunniens*) in Caddo Lake by the Texas Department of State Health Services (TXDSHS), because both species have mean Hg concentrations above the TXDSHS comparison value of 700 ng/g wet weight (largemouth bass: mean, 734 ng/g wet wt; range, 169–1,770 ng/g wet wt; freshwater drum: mean, 1,119 ng/g wet wt; range, 302–1620 ng/g wet wt) [21]. The Louisiana Department of Environmental Quality (LADEQ) monitors largemouth bass and freshwater drum on the Louisiana side of Caddo Lake. The LADEQ has not issued an advisory, however, because the mean concentrations of Hg in these species do not exceed 500 ng/g wet weight, the level at which the LADEQ considers issuing advisories (largemouth bass: mean, 335 ng/g wet wt; range, below detection limit to 1,088 ng/g wet wt; freshwater drum: mean, 357 ng/g wet wt; range, 82.3–691 ng/g wet wt) (LADEQ, http://www.deq.louisiana.gov/portal/default.aspx?tabid=1637).

Fish and invertebrate collection

We collected fish using two techniques, gill netting and electrofishing, with assistance from Texas Parks and Wildlife Department fisheries biologists. Fish were collected using a gill net from eight sites (all in open-water habitat). Nets were deployed in the late afternoon on May 10, 2004, and were retrieved the following morning. Gill nets were 38 m in length by 2.4 m in depth and were constructed of monofilament webbing. Each net consisted of five panels that were 7.6 m in length, with bar measures ranging from 25 to 76 mm. Fish were collected with a boat-mounted electrofishing unit from nine additional sites (five sites in wetland and four sites in open-water habitat) during the early evening of May 10, 2004, and the morning of May 12, 2004. After collection, fish were placed on ice and transported to a laboratory where TL was measured and otoliths removed. Fish were then frozen for subsequent Hg and stable isotope analyses.

We assumed that fish were resident in the habitat from which they were collected. Studies of home range and movement have been conducted for largemouth bass, spotted gar (*Lepisosteus osseous*), and bluegill (*Lepomis macrochirus*) in other systems, and those results support this assumption. Based on a study of activity patters of largemouth bass in a shallow (mean depth, 3.0 m) reservoir in the southern United States, Sammons and Maceina [22] concluded that largemouth bass in large systems are relatively sedentary and spend much of their time in small (<5 ha) areas despite an abundance of available habitat. Other studies also have suggested that largemouth bass home ranges are small, from 0.01 to 5.16 ha [23,24]. Snedden et al. [25] studied spotted gar movement and habitat use using radio telemetry in the Atchafalaya River Basin (LA, USA), which contains a diversity of connected aquatic habitats, including shallow open-water lakes, stagnant backwater areas with dense aquatic vegetation, natural bayous, and man-made canals. Spotted gar established relatively small home ranges during summer and fall–winter (range, 1.0–77.9 ha; median, 6.6 ha), typically 2 km from the site at which the individual was initially captured and tagged. In the Atchafalaya River Basin, the home ranges of spotted gar increased considerably during seasonal inundation of the flood plain. Flows into Caddo Lake are regulated, however, and flooding rarely occurs. Parsons and Reed [26] used a mark–recapture study to examine the movement of bluegill among interconnected lakes in Minnesota, USA. For bluegill tagged in Victoria Lake (1.7 km^2), 86% of the tags recovered were from fish recaptured within Victoria Lake. In the present study, all sampling sites in the wetland habitat were more than 2 km away from sampling sites in the open-water habitat.

Stable isotope ratios of nitrogen and carbon in fish can be used to infer trophic relationships when interpreted relative to isotope ratios in primary consumers [27]. We collected surfacing-grazing gastropods and unionid mussels as representative primary consumers [28]. Gastropods reflect the isotopic signature of the detritus and periphyton that form the base of littoral food webs, and mussels reflect the isotopic signature of seston (includes phytoplankton), which forms the base of pelagic food webs [28]. Gastropods and unionid mussels were collected by hand or with a dip-net from one site in the wetland habitat (n = 5 and 6, respectively) and one site in the open-water habitat (n = 1 and 5, respectively) on May 18, 2004. After collection, gastropods and unionid mussels were frozen until processing for stable isotope analyses.

Analysis of Hg

Fillets were dissected from each fish, and a small subsample of epaxial muscle was collected from the center of each fillet. Total Hg concentrations in fish tissues were analyzed with a direct Hg analyzer (DMA-80; Milestone) that uses thermal decomposition, gold amalgamation, and atomic absorption spectrometry [29], and these concentrations are reported as ng total Hg/g wet weight fish. We used total Hg as a proxy for MeHg, the predominant form of Hg in fish [10]. Additional information concerning Hg analyses, including quality-assurance data, are provided in a previous study [19].

Age analyses

We counted otolith annuli to estimate the age of each fish using the methods described by Boxrucker [30] for bluegill and redear sunfish (*Lepomis microlophus*); Buckmeier et al. [31] for channel catfish (*Ictalurus punctatus*); Buckmeier and Howells [32] for largemouth bass, white bass (*Morone chrysops*), yellow bass (*Morone mississippiensis*), chain pickerel (*Exos niger*), and gizzard shad (*Dorosoma cepedianum*); Ferrara [33] for spotted gar; and the Fish and Wildlife Research

Institute (http://research.myfwc.com/features/view_article.asp?id=22709) for freshwater drum. Two readers independently estimated the ages of fish without knowledge of the TL of the fish, and disagreements were resolved by reexamining otoliths and mutually agreeing on age. We estimated the age of a subset of largemouth bass (33 from wetland and 32 from open-water habitats). For all other species, we determined the age of every individual.

Trophic position and diet analyses

Stable nitrogen and carbon isotope ratios of fish and primary consumer muscle tissue were used to assess the food-web position of individual fish. Stable nitrogen isotopes are used differentially in cellular processes, resulting in a predictable increase in the heavy isotope, ^{15}N, relative to ^{14}N with each increase in vertical trophic level, and these isotopes can be used to assess trophic position [34]. Stable carbon isotopes (^{13}C and ^{12}C) can be used to determine whether fish feed in food webs based on pelagic (i.e., those based on phytoplankton) or littoral (i.e., those based on periphyton) primary production, because phytoplankton tends to be less enriched with ^{13}C compared to periphyton [35,36]. Stable carbon isotopes cannot be used to distinguish between wetland and open-water habitat use, because both habitat types contain littoral and pelagic primary producers.

Different tissues have different isotope turnover rates [37], so we analyzed isotope ratios in muscle tissues for both fish and invertebrates to minimize error. Fish fillet subsamples and foot muscle from individual gastropods and unionid mussels were dried in a 60°C oven and homogenized using a ball mill grinder. Sixty-one largemouth bass (31 from wetland and 30 from open-water habitats) were analyzed at Louisiana State University (Baton Rouge, LA, USA) for isotopic composition using a Delta Plus isotope ratio mass spectrometer (Thermo Finnigan MAT). The remaining largemouth bass (13 from wetland and 17 from open-water habitats) and all other fish and primary consumers were analyzed at the University of California–Davis (CA, USA) stable isotope facility using a Hydra 20/20 continuous-flow isotope ratio mass spectrometer (PDZ Europa) as described by Chumchal et al. [19]. Carbon and nitrogen isotope results are given as

$$\delta^{13}C \text{ or } \delta^{15}N = (R_{\text{sample}}/R_{\text{standard}} - 1)\cdot 1,000$$

where R is $^{13}C/^{12}C$ for $\delta^{13}C$ and $^{15}N/^{14}N$ for $\delta^{15}N$. Standards for $\delta^{13}C$ and $\delta^{15}N$ were Vienna Pee Dee Belemnite and air N_2, respectively. Mean uncorrected $\delta^{15}N$ and $\delta^{13}C$ values of all fish and invertebrates examined in the present study are presented in *Supporting Information*, Table S1 (http://dx.doi.org/10.1897/08-197.S1).

To calculate trophic position of individual fish, $\delta^{15}N$ values in fish were first corrected for habitat-specific differences in basal $\delta^{15}N$ using $\delta^{15}N$ and $\delta^{13}C$ values of gastropods and unionid mussels according to the method described by Post [27]. Because we assumed that fish were resident in the habitat where they were collected, $\delta^{15}N$ values of fish were corrected for differences in $\delta^{15}N$ at the base of the food web using both gastropods and unionid mussels collected from the same habitat. We then calculated trophic position for individual fish from corrected $\delta\ ^{15}N$ values assuming an increase of 3.4‰ per trophic level [27]. We corrected $\delta^{13}C$ of fish for trophic enrichment according to the method described by Fry [34]. A detailed description of methods used to calculate trophic position and corrected $\delta^{13}C$ values for fish appear in a previous study [19]. We visually compared the $\delta^{13}C$ values of primary consumer to the $\delta^{13}C$ values of fish and made a qualitative assessment as to whether fish were feeding predominately in pelagic or littoral food webs.

Statistical analyses

Between-species comparisons. To determine which ecological factors were related to Hg contamination in the Caddo Lake fish assemblage (between-species variation), we used a series of analysis of covariance (ANCOVA; SPSS, Ver 11.5.0; SPSS) models to determine the effect of habitat (categorical variable) and a covariate (mean TL, age, trophic position, or $\delta^{13}C$) on mean log-transformed Hg concentration (dependent variable) [38]. In ANCOVA models, the effect of the covariate on the dependent variable is removed from the unexplained variability by regression analysis. The final ANCOVA tests the difference between treatment means, adjusted for the effect of the covariate [38]. For all covariates, the slopes of the relationships between the covariate and mean log-transformed Hg were homogeneous between habitats (habitat × covariate, $p > 0.05$), so we removed the interaction term from the model and tested for main effects of habitat and the covariate. We also used a general linear model (GLM) to test the predictive power of multiple explanatory variables on Hg concentration. Specifically, we examined the effect of habitat (categorical variable) and mean TL, age, trophic position, and $\delta^{13}C$ (covariates) on mean log-transformed Hg concentration.

Within-species comparisons. For each species of fish, we used linear regression to determine the relationship between TL, age, trophic position, $\delta^{13}C$, and Hg concentration. To help explain patterns in fish Hg concentration, we also used linear regression to examine the relationships between fish trophic position and TL and between fish $\delta^{13}C$ values and TL. We used a series of ANCOVA models to explore habitat-specific differences in Hg concentration, trophic position, and $\delta^{13}C$ values for fish species that were collected from both wetland and open-water habitats and for which sample size was five or more individuals from each habitat. For each species of fish, we compared Hg concentration, trophic position, or $\delta^{13}C$ (dependent variables) between habitats (categorical variable), with fish TL or age as covariates. We do not present data regarding within-species variation in Hg concentration for largemouth bass, because similar analyses appear elsewhere [19]. In some cases, the slopes of the relationships between the covariate and dependent variable were not homogenous (an assumption of ANCOVA), so we tested for main effects of habitat and the covariate with the interaction term included in the model and performed the Wilcox procedure [38]. The Wilcox procedure determines the range of the covariate for which a significant habitat effect exists (WILCOX, Ver 3.2; http://www.zoology.unimelb.edu.au/qkstats/software.html). Finally, we used GLMs to test the predictive power of multiple explanatory variables on Hg concentration for each species of fish. Specifically, we examined the effect of habitat (categorical variable) and TL, age, trophic position, and $\delta^{13}C$ (covariates) on mean log-transformed Hg concentration. Statistical significance was determined at $p \leq 0.05$ unless otherwise noted. To account for repeated tests with Hg as the dependent variable, we used the Bonferonni procedure to adjust significance levels to $p \leq 0.05/c$, where c is the number of comparisons in the family [38].

RESULTS

Total length, age, trophic position, $\delta^{13}C$ values, and Hg concentration exhibited substantial variation within the fish

Table 1. Descriptive statistics for species examined, including mean ± 95% confidence interval for independent variables and Hg concentration

Species	n^a	Total length (mm)	Age (years)	Trophic position	$\delta^{13}C$	Hg (ng/g wet wt)
Forested wetland						
Spotted gar	5	542 ± 70	5.2 ± 1.1	4.5 ± 0.1	−29.8 ± 0.5	833 ± 136
Chain pickerel	6	403 ± 79	2.7 ± 1.1	4.0 ± 0.2	−29.6 ± 0.8	500 ± 216
Channel catfish	3	352 ± 59	4.3 ± 1.7	3.3 ± 0.4	−29.1 ± 0.4	105 ± 27
Freshwater drum	6	439 ± 24	8.0 ± 0	4.0 ± 0.2	−29.6 ± 0.9	600 ± 177
Yellow bass	5	141 ± 29	1.8 ± 1.1	3.4 ± 0.2	−30.5 ± 0.5	61.5 ± 36
Largemouth bass	44^b	287 ± 37	3.9 ± 0.7	4.1 ± 0.1	−29.6 ± 0.3	465 ± 113
Bluegill	6	164 ± 17	3.7 ± 0.7	3.9 ± 0.2	−30.9 ± 1.2	180 ± 52
Redear sunfish	13	193 ± 15	4.2 ± 0.7	3.4 ± 0.2	−30.7 ± 0.7	234 ± 54
Open water						
Spotted gar	19	603 ± 48	5.6 ± 0.6	4.4 ± 0.1	−29.7 ± 0.2	474 ± 91
Gizzard shad	29	345 ± 19	5.1 ± 0.5	3.3 ± 0.1	−29.5 ± 0.5	30.7 ± 3.7
Channel catfish	27	385 ± 35	4.4 ± 0.5	3.5 ± 0.1	−29.7 ± 0.3	139 ± 40
Freshwater drum	18	409 ± 25	7.1 ± 1.2	3.9 ± 0.2	−29.3 ± 0.4	319 ± 120
White bass	21	347 ± 23	3.2 ± 0.7	4.0 ± 0.1	−28.7 ± 0.3	262 ± 78
Yellow bass	39	217 ± 11	3.2 ± 0.2	3.7 ± 0.0	−29.8 ± 0.2	104 ± 15
Largemouth bass	47^b	260 ± 33	2.6 ± 0.5	4.2 ± 0.1	−30.0 ± 0.3	193 ± 54
Bluegill	14	150 ± 11	2.6 ± 0.4	3.6 ± 0.2	−29.4 ± 0.3	81.4 ± 20
Redear sunfish	5	170 ± 34	2.6 ± 0.5	3.2 ± 0.2	−30.2 ± 0.2	127 ± 76

[a] n = total number of fish collected.

[b] Age was determined for a subset of largemouth bass (33 from wetland and 32 from open-water habitats).

assemblage (Table 1). Mean TL of fish examined in the present study ranged from 141 mm (yellow bass collected from wetland habitats) to 603 mm (spotted gar collected from open-water habitats). Mean age ranged from 1.8 years (yellow bass collected from wetland habitats) to eight years (freshwater drum collected from wetland habitats). Fish spanned one trophic level from secondary to tertiary consumers (trophic level 3 and 4, respectively). Most fish species had mean $\delta^{13}C$ values that were similar to those of gastropods or intermediate between those of gastropods and unionid clams, indicating that they fed in food webs based on littoral primary production or fed on both littoral and pelagic production, respectively (*Supporting Information*, Table S1; http://dx.doi.org/10.1897/08-197.S1). Mean Hg concentrations ranged from 61.5 ng/g wet weight (yellow bass collected from wetland habitats) to 833 ng/g wet weight (spotted gar collected from wetland habitat).

Between-species comparisons

Mean log-transformed Hg concentrations of Caddo Lake fish were significantly and positively related to mean trophic position and TL but were not significantly related to age or $\delta^{13}C$ values (Table 2). Fish collected from wetland habitats had significantly higher concentrations of Hg compared to fish collected from open-water habitats even after statistically controlling for the effect of TL or trophic position (Table 2 and Fig. 1). To build a model predicting Hg concentration in Caddo Lake fish, we used a GLM that included mean fish trophic position, $\delta^{13}C$ values, TL, age, and habitat. These variables explained most of the variation in log-transformed Hg concentration (GLM: degrees of freedom [df] = 5, 11; $f = 8.19$; $p = 0.002$; $r^2 = 0.79$), but only trophic position (GLM: df = 1, 11; $f = 11.6$; $p = 0.006$; partial $\eta^2 = 0.51$) and habitat (GLM: df = 1, 11; $f = 6.01$; $p = 0.032$; partial $\eta^2 = 0.35$) were significantly related to log-transformed Hg concentration in the Caddo Lake fish assemblage. Even with all covariates included in the model, trophic position explained 51% of the variation in mean Hg concentration. Habitat explained 35% of the variation in Hg concentration, with fish from the wetland habitat having higher concentrations of Hg compared to fish from the open-water habitat. To determine if size differences between fish could account for a significant amount of variation in Hg concentrations after accounting for habitat and trophic position, we examined an additional model that included mean fish trophic position, TL, and habitat (GLM: df = 3, 13; $f = 14.9$; $p < 0.001$; $r^2 = 0.77$). Like in the full model, only trophic position (GLM: df = 1, 13; $f = 12.4$; $p = 0.004$; partial $\eta^2 = 0.49$) and habitat (GLM: df = 1, 13; $f = 8.15$; $p = 0.014$; partial $\eta^2 = 0.39$) were significantly related to log-transformed Hg concentration in the Caddo Lake fish assemblage. This indicates that TL differences between species did not influence our results.

Table 2. Significance values associated with analysis of covariance (ANCOVA)[a]

Covariate[b]	Covariate × habitat (p)	ANCOVA (p)	
		Habitat	Covariate
Total length	0.42	0.03	0.003
Age	0.48	0.1	0.07
Trophic position	0.62	0.02	<0.001
$\delta^{13}C$	0.84	0.06	0.30

[a] Dependent variable was mean log-transformed Hg concentration.

[b] Covariates are species averages.

Within-species comparisons

For many species, variation in Hg concentration was best explained by TL or age; however, we found significant correlations between Hg and trophic position and between Hg and $\delta^{13}C$ values in some species (Table 3). For most species, TL, age, trophic position, and $\delta^{13}C$ values were positively correlated with Hg concentration. One exception was the inverse relationship between Hg concentration and $\delta^{13}C$ values in spotted gar collected from wetland habitats.

To help explain patterns in Hg concentration, we also examined the relationships between fish trophic position and TL and between fish $\delta^{13}C$ values and TL. Trophic position and $\delta^{13}C$ values were positively and significantly correlated with

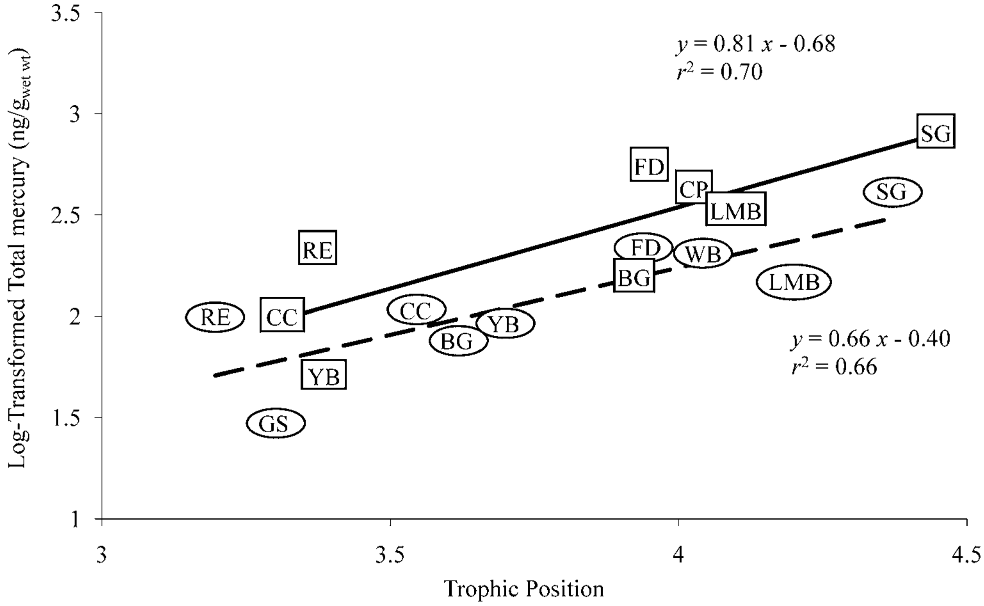

Fig. 1. Relationship between mean log-transformed Hg and mean trophic position. Markers with square borders and a solid trend line represent fish collected from wetland habitats. Markers with oval borders and a dashed trend line represent fish collected from open-water habitats. BG = bluegill; CC = channel catfish; CP = chain pickerel; FD = freshwater drum; GS = gizzard shad; LMB = largemouth bass; SG = spotted gar; RE = redear sunfish; WB = white bass; YB = yellow bass.

TL in several species (Table 3). The $\delta^{13}C$ values were inversely and significantly correlated with TL in largemouth bass from wetland habitats.

We collected five or more spotted gar, freshwater drum, yellow bass, redear sunfish, and bluegill from each habitat, which allowed us to compare Hg concentrations and ecological characteristics of these species between habitats. Mercury concentrations were significantly higher in fish from the wetland habitat after statistically controlling for TL and age for all species except redear sunfish (Table 4 and Fig. 2). For all fish species, trophic position and $\delta^{13}C$ values were either lower in fish collected from wetland habitats or not significantly different between habitat types after statistically controlling for TL (Table 4, Fig. 2).

To build models predicting Hg concentration in each species of Caddo Lake fish, we used GLMs that included trophic position, $\delta^{13}C$, TL, age, and habitat. These models explained 79 to 90% of the variation in log-transformed Hg concentration (Table 5). Total length, age, and habitat were significant predictors of log-transformed Hg concentration for three of the five species examined. Trophic position was a significant predictor of log-transformed Hg concentration in only one of the species examined. Carbon isotope values were not a significant predictor of Hg for any species when other variables were included in the model.

DISCUSSION

Trophic position was the best predictor of Hg concentration in the Caddo Lake fish assemblage. Mercury was biomagnified with each trophic level, whereby tertiary consumers had mean Hg concentrations that were approximately fivefold higher than those of secondary consumers. The slope of the relationship between mean log-transformed Hg concentration and mean trophic position (determined using $\delta^{15}N$) is a measure of biomagnification and can be used to compare transfer efficiencies between Hg and biomass in food webs [39–41]. A slope of greater than zero indicates that Hg is transferred more efficiently than biomass through the food web—in other words, that biomagnification is occurring [39]. In the present study, the food-web magnification factors (the slopes of the relationship between mean log-transformed Hg concentration and mean trophic position [41]) for the wetland and open-water habitats were 0.81 and 0.66, respectively, which are equivalent to enrichment factors (the slope of the relationship between mean log-transformed Hg concentration and mean $\delta^{15}N$ values and the value most commonly reported in the literature [41]) of 0.24 and 0.19, respectively. These values indicate that Hg increased by a factor of five to six with each increase in trophic level in the Caddo Lake fish assemblage. The enrichment factors observed in the present study are similar to those reported in other studies (0.21 [42] and 0.28 [43]) conducted in subtropical ecosystems. To our knowledge, the present study is the only examination of enrichment factors in the subtropical United States and is one of the few that have examined enrichment factors outside the temperate or sub-Arctic region [44]. Riget et al. [44] reviewed enrichment factors from studies conducted in diverse systems, including freshwater and marine ecosystems located in Arctic and tropical regions, and those authors found that the enrichment factors were consistent. The similarities between the enrichment factors observed in the present study and those observed in other studies suggest that enrichment factors might be similar across all regions and aquatic ecosystems [44].

Although trophic position was the most important predictor of Hg concentration between fish species, it generally was a weak predictor of Hg concentrations within species, because most individuals of a given species had similar trophic positions. This is not surprising, because the fish examined in the present study were all older than one year. The size of prey items that a fish can consume increases throughout its life, because fish are gape-limited predators with indeterminate growth [45]. In many species, however, major ontogenetic diet shifts (the shift from zooplankton feeding to invertebrate feeding or invertebrate feeding to piscivory) occur within the first

Table 3. Pearson's correlation coefficients (*r*) for the relationships between Hg and ecological characteristics[a]

Species	Hg vs total length	Hg vs age	Hg vs trophic position	Hg vs $\delta^{13}C$	Trophic position vs total length	$\delta^{13}C$ vs total length
Forested wetland						
Spotted gar	0.43	−0.11	0.20	*−0.99*	−0.48	−0.36
Chain pickerel	0.87	*0.94*	0.18	0.83	0.59	0.69
Channel catfish	0.44	−0.05	0.90	−0.98	0.01	−0.61
Freshwater drum	0.37	—	0.80	0.30	0.60	0.16
Yellow bass	*0.97*	0.91	0.21	0.90	0.35	*0.91*
Largemouth bass	*0.87*	*0.89*	*0.55*	−0.23	*0.61*	*−0.40*
Bluegill	0.69	0.74	0.52	0.11	0.55	0.40
Redear sunfish	0.56	*0.89*	−0.03	−0.17	0.07	0.33
Open water						
Spotted gar	*0.71*	*0.59*	*0.78*	0.13	*0.69*	0.01
Gizzard shad	−0.25	−0.32	−0.34	−0.36	*0.69*	*0.73*
Channel catfish	*0.66*	*0.67*	0.34	0.28	0.13	*0.57*
Freshwater drum	*0.92*	*0.65*	*0.85*	−0.01	*0.83*	−0.11
White bass	*0.68*	*0.93*	0.50	0.31	*0.88*	*0.67*
Yellow bass	*0.81*	*0.91*	0.15	*0.45*	0.19	*0.76*
Largemouth bass	*0.74*	*0.85*	*0.74*	0.36	*0.74*	*0.63*
Bluegill	0.52	*0.92*	0.18	0.14	0.29	0.35
Redear sunfish	0.83	0.83	0.12	0.88	0.11	0.70

[a] Numbers in italic indicate a significant correlation. To account for repeated tests with mercury as the dependent variables ($n = 4$ per species), α was reduced to 0.0125 (0.05/4) when Hg was the dependent variable. For other tests, $\alpha \leq 0.05$.

year of life [45–47]. The species that exhibited a positive Hg–trophic position relationship (largemouth bass, spotted gar, and freshwater drum) also exhibited positive trophic position–TL relationships, indicating that as they increased in size, they fed on organisms higher in the food web. Largemouth bass, spotted gar, and freshwater drum are large-bodied predators whose diets become increasingly dependent on fish as they grow, with largemouth bass and spotted gar feeding almost exclusively on fish as adults [48,49]. Results from our present study indicate that trophic position has limited utility for predicting within-species Hg concentrations of adult fish unless they exhibit ontogenetic diet shifts.

In contrast to studies conducted in other lakes [7–9], we found no relationship between $\delta^{13}C$ values and Hg concentration in the Caddo Lake fish assemblage. The lack of a relationship between $\delta^{13}C$ values and Hg concentration in fish was surprising, and it may result from the lack of variation in $\delta^{13}C$ values. The fish assemblage of Caddo Lake had relatively similar mean $\delta^{13}C$ values (Table 1) that were intermediate between those of primary consumers of littoral and pelagic carbon (*Supporting Information*, Table S1; http://dx.doi.org/10.1897/08-197.S1), indicating a high degree of omnivory. Fish communities in vegetation-dominated, shallow lakes are characterized by high levels of omnivory [50–52], in contrast to deep lakes that contain species that feed preferentially within food webs based on pelagic or littoral sources of primary production [53]. Studies that found a relationship between $\delta^{13}C$ values and Hg concentration in fish were conducted in relatively deep lakes (11–700 m) [7–9]. We hypothesize that unlike in deep lakes, $\delta^{13}C$ values are not an important predictor of Hg concentration in fish assemblages from shallow, vegetation-dominated lakes and reservoirs.

Within species, the nature of the $\delta^{13}C$-Hg relationships in the present study also were different than those observed in previous studies. We found no relationship between $\delta^{13}C$ values and Hg concentration for most species. In yellow bass collected from open-water habitats, we found a positive relationship between $\delta^{13}C$ values and Hg, indicating that individuals more connected to littoral food webs were more contaminated with Hg compared to individuals connected to pe-

Table 4. Significance values associated with analysis of covariance used to compare Hg and other ecological variables in species of fish collected from both habitats[a]

	Hg vs TL (*p*)		Hg vs age (*p*)		Trophic position vs TL (*p*)		$\delta^{13}C$ vs TL (*p*)	
Species	Habitat	TL	Habitat	Age	Habitat	TL	Habitat	TL
Spotted gar	<0.001	<0.001	<0.001	0.02	—[b]	0.004	0.5	0.6
Freshwater drum	0.03	<0.001	—[c]	—[c]	0.2	<0.001	0.6	0.8
Yellow bass	0.007	<0.001	—[d]	<0.001	0.01	0.2	0.1	<0.001
Redear	0.2	0.008	0.9	<0.001	0.8	0.5	0.2	0.2
Bluegill	<0.001	0.01	0.007	<0.001	0.1	0.2	0.002	0.2

[a] For each comparison, the main effect of habitat and the covariate (total length [TL] or age) is shown. To account for repeated tests with Hg as the dependent variables ($n = 2$ per species), α was reduced to 0.025 (0.05/2) when Hg was the dependent variable. For other tests, $\alpha \leq 0.05$.

[b] The assumption of homogeneity of slopes was violated. Therefore, we used the Wilcox procedure to look for differences in TL-specific trophic position between habitats and found no significant differences ($p > 0.05$) for spotted gar longer than 528 mm.

[c] Analysis was not possible, because all freshwater drum collected from wetland habitats were the same age.

[d] The assumption of homogeneity of slopes was violated. Therefore, we used the Wilcox procedure to look for differences in age-specific Hg concentration between habitats and found no significant differences ($p > 0.05$).

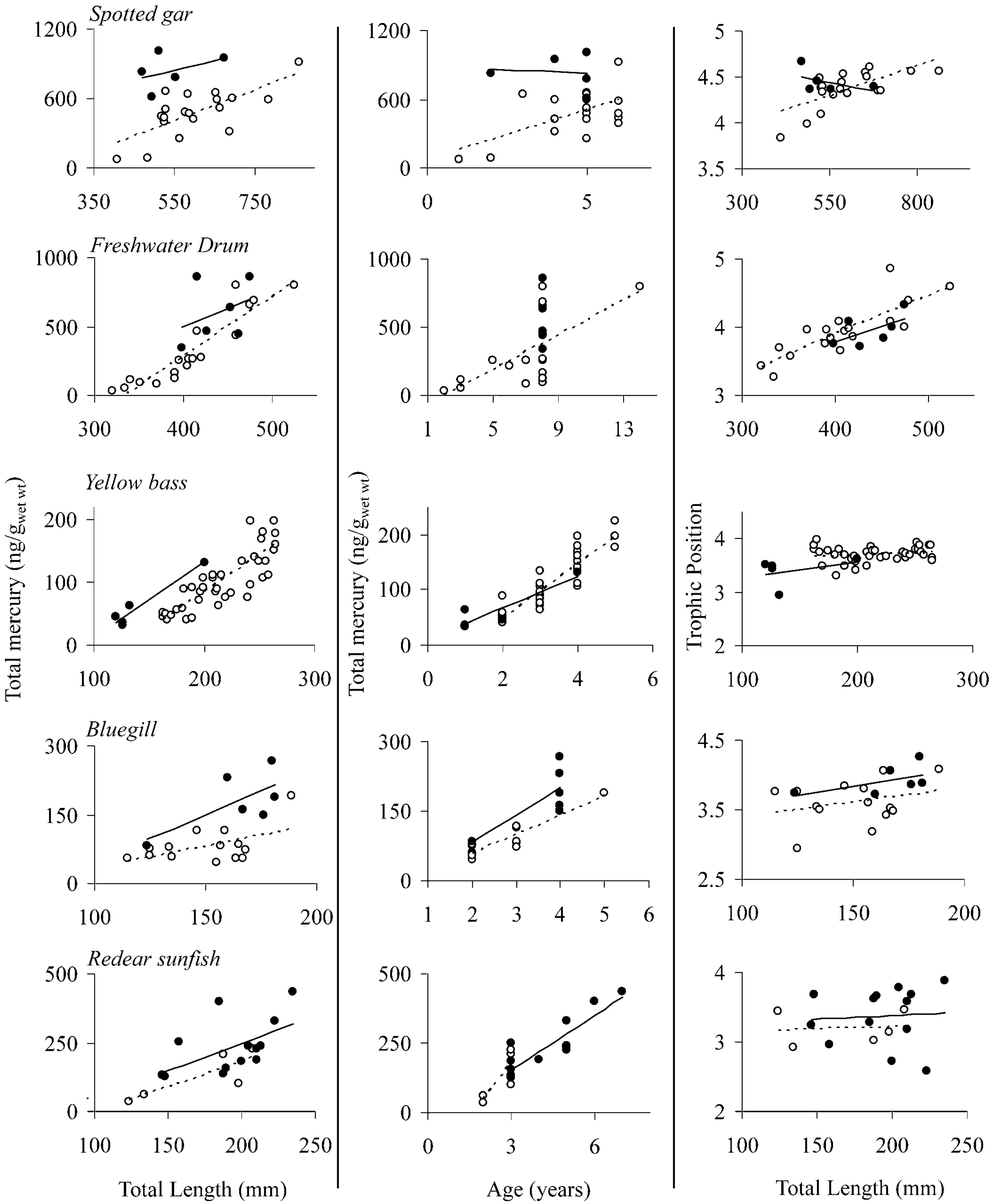

Fig. 2. Relationships between total length (TL) and total (Hg, age and total Hg, and trophic position and TL in spotted gar, freshwater drum, yellow bass, bluegill, and redear sunfish collected from forested-wetland (● solid line) and open-water (○ dashed line) habitats.

lagic food webs. This finding is in contrast to previous studies that have found negative relationships between δ^{13}C values and Hg concentration in fish (i.e., fish connected to pelagic food webs were more contaminated with Hg). As discussed above, however, previous studies were conducted in large, deep lakes with extensive pelagic zones [7–9]. In shallow ecosystems, littoral zones are important sites of Hg methylation [54]; therefore, fish that are dependent on periphyton-based food

Table 5. Results from general linear models examining the effect of multiple independent variables (total length, age, trophic position, $\delta^{13}C$ values, and habitat) on log-transformed Hg concentration[a]

Species	Variable	r^2	p	Partial η^2
Spotted gar	Model	0.83	<0.001	
	Age		0.02	0.26
	Trophic position		0.001	0.48
	Habitat		0.002	0.43
Freshwater drum	Model	0.88	<0.001	
	Total length		0.005	0.36
	Habitat		0.008	0.33
Yellow bass	Model	0.87	<0.001	
	Total length		0.009	0.17
	Age		<0.001	0.34
Bluegill	Model	0.90	<0.001	
	Age		<0.001	0.70
	Habitat		0.02	0.35
Redear sunfish	Model	0.79	0.001	
	Total length		0.05	0.28

[a] For each species, statistics associated with the full model and variables that had a significant main effect ($p \leq 0.05$) on log-transformed Hg concentration are presented.

webs may be more contaminated with Hg. Similar to the pattern observed during other studies, however, we found a negative relationship between $\delta^{13}C$ values and Hg concentration in spotted gar.

Although TL and age were weak predictors of between-species variation in Hg concentration of fish, they were the best predictors of Hg concentration within species. The concentration of Hg in fish tissues often has been observed to increase with age and body size of fish [10], and at least three compatible mechanisms have been hypothesized to be responsible for this pattern. First, the slow rate of elimination of MeHg by fish relative to its rapid uptake is hypothesized to lead to an increase in the Hg concentration of fish tissue with age (and size) even if dietary concentrations of Hg remain constant [10]. Second, as fish get older and increase in size, they have the ability to consume larger, more contaminated diet items [3]. Third, as fish grow, they undergo ontogenetic diet shifts to higher-trophic-position prey, which exposes them to higher concentrations of Hg [55]. As discussed above, the trophic positions of largemouth bass, spotted gar, and freshwater drum increased with TL, which means that the third mechanism is a potential explanation for the positive Hg–TL and Hg–age relationships observed for these species. We, however, collected several species of fish (channel catfish, yellow bass, and bluegill) whose trophic position did not increase with TL, yet they exhibited a positive Hg–TL relationship. This indicates that for some species, the increase in Hg concentration with TL and age cannot be explained by a shift in diet to prey items with higher trophic positions (third mechanism). As discussed previously, the third mechanism is less likely to be important in studies focused on adult fish. We were not able to distinguish between the other hypothesized mechanisms using our data, and more studies are needed to determine if the increase in Hg concentration with size in Caddo Lake fish results from time-related bioaccumulation, a tendency for fish to consume larger prey items as they grow, or some combination of both.

The habitat from which fish were collected was an important predictor of Hg concentrations in their tissues, with fish from wetlands exhibiting higher concentrations of Hg compared to fish from open-water habitats. Relative to the number of studies that have examined Hg contamination of fish in lakes (Mercury Bibliography, http://www.bio.tcu.edu/faculty/drenner/mercury.htm), there have been relatively few reports of spatial or habitat variation (for review, see Chumchal et al. [19]). This may be because habitat-specific variation in Hg concentration of fish is rare or not evaluated in most studies. Several factors could have led to habitat-specific differences in Hg contamination in Caddo Lake. Ecosystems with high MeHg availability contain food webs that are highly contaminated with Hg [10]; therefore, habitat-specific differences in Hg concentration could be caused by differences in MeHg availability between habitats. Because fish size, age, and food-web position all influence Hg contamination, however, differences in these ecological factors between habitats also could lead to habitat-specific differences in Hg concentrations of fish. In a previous study, we hypothesized that high concentrations of Hg in largemouth bass from the wetland most likely resulted from elevated Hg availability in this habitat rather than from differences in ecological characteristics of bass between habitats [19]. Below, we discuss two approaches using data from the additional fish species examined in the present study to distinguish between these alternative hypotheses.

In the first approach, we used the method described by Jardine et al. [41] to determine if a difference in trophic position or baseline contaminant levels was responsible for differences in fish Hg concentrations between habitats. As discussed above, the slope of the relationship between mean Hg concentration and mean trophic position is a measure of biomagnification [39–41]. The y-intercept of the relationship between mean Hg concentration and mean trophic position can be used to estimate the concentration of Hg at the base of the food web [40,41]. Comparing the slopes of the relationships between mean log-transformed Hg and trophic position between habitats revealed that biomagnification was similar between habitats (the slopes were not significantly different) [41]. The y-intercepts of the relationship between mean log-transformed Hg and mean trophic position, however, were significantly different between habitats, which indicates that the level of Hg at the base of the food web was elevated in the wetland habitat [40,41]. This finding complements the results from a previous study in which we examined Hg concentrations in Mississippi grass shrimp (*Palaemonetes kadiakensis*) as a proxy for Hg contamination at the base of the food web [19] and found elevated concentrations of total Hg in shrimp collected from wetland habitats (mean ± 95% confidence interval, 69.5 ± 6.2 ng/g wet wt) relative to those from open-water habitats (57.4 ± 5.0 ng/g wet wt) [19]. Like other wetland ecosystems, the wetlands in Caddo Lake have features that may make them conducive to Hg availability and methylation [10,11]. Briefly, relative to open-water habitats, wetland habitats in Caddo Lake have low pH [56], low dissolved oxygen concentrations [56], and high organic carbon in sediments [57]. In contrast to open-water habitats, wetland habitats in Caddo Lake have direct connections to seasonally flooded areas [18].

Our second approach was to compare characteristics of individual fish species between the two habitats. A similar analysis is presented for largemouth bass in a previous paper [19]. All species of fish collected from wetland habitats for which sample size was large enough to make habitat comparisons, except redear sunfish, had significantly higher concentrations of Hg after statistically adjusting for TL and age differences using ANCOVA models. This finding indicates that TL or age differences cannot explain patterns in Hg concentrations between habitats. Furthermore, the trophic positions of fish collected from the wetland habitat were lower or not significantly different than the trophic positions of fish collected from the open-water habitats after statistically adjusting for TL. Not only were the differences in trophic position between habitats small, the trophic position was slightly elevated in the open-water habitat, which is the opposite of what would be expected if trophic position was responsible for the elevated concentrations of Hg in fish from the wetland habitat. Finally, for all species except bluegill, $\delta^{13}C$ values were not significantly different between habitats; thus, differences in horizontal food-web position cannot explain the differences in Hg between habitats. The results for the five species examined in the present study are similar to those of largemouth bass presented in a previous study [19]. This is worth noting, because the six species examined in the two studies exhibit diverse natural histories, ranging from relatively small-bodied insectivores (bluegill and redear sunfish) to large-bodied piscivores (spotted gar and largemouth bass) [48]. These data indicate that elevated concentrations of Hg in fish from the wetland habitat cannot be explained by differences in the ecological characteristics of fish between habitats and supports the hypothesis that MeHg availability is higher in the wetland habitat.

A secondary objective of the present study was to compare Hg concentrations of fish from Caddo Lake to U.S. EPA benchmarks designed to protect human and wildlife health. Spotted gar, chain pickerel, freshwater drum, and largemouth bass had concentrations of Hg that exceeded the U.S. EPA screening value (300 ng/g wet wt) [58]. The screening value is derived from a reference dose determined from epidemiological studies and is predicted to be the level of Hg that can be safely consumed by humans over a lifetime. Wetland habitats should be of particular concern to public health officials, because half the species collected from this habitat had mean Hg concentrations exceeding the screening value. We recommend that Hg concentrations be monitored in chain pickerel and spotted gar. Neither of these species have fish consumption advisories, yet both had concentrations of Hg similar to those of freshwater drum and largemouth bass, two species that currently have fish consumption advisories. Although directed effort by Caddo Lake anglers to catch chain pickerel is low, they frequently are caught by anglers targeting other species [15]. To our knowledge, no data are available regarding the use of spotted gar by Caddo Lake anglers.

In addition to potential negative impacts on human health, elevated Hg concentrations in wetland habitats could be negatively impacting fish and wildlife health. Fish with whole-body concentrations of Hg from 200 to 1,000 ng/g wet weight (muscle concentrations, 326–1,630 ng/g wet wt [11]) may be at risk for negative health effects [59]. In laboratory experiments, fish with whole-body concentrations of Hg between 440 to 864 ng/g wet wt (muscle concentrations, 717–1,408 ng/g wet wt [11]) had reduced hormone levels [60], reproductive success [60], and weight of offspring [61] as well as altered predator avoidance behavior [62]. In a field study, northern pike (*Esox lucius*) with Hg concentrations of 69 to 622 ng/g wet wt in their muscle tissue had livers that contained lipofuscin, a pigment that results from oxidative stress [63]. The Hg concentrations of most fish from Caddo Lake were below levels observed to result in negative health effects; however, some individuals within the fish assemblage, especially tertiary consumers from wetland habitats, had concentrations of Hg similar to those that have been found in laboratory and field studies to negatively impact fish health. Future studies should assess the health of spotted gar in the wetland habitat, because most individuals from this population had Hg concentrations above levels found to negatively impact fish health.

In the wetland habitat, most species of fish exceeded critical values developed by the U.S. EPA's Great Lakes Water Quality Initiative for protecting piscivorous wildlife health [64]. The U.S. EPA's wildlife critical values correspond to fish whole-body Hg concentrations of 100 and 200 ng/g wet weight (equivalent to muscle concentrations of 163–326 ng/g wet wt [11]) for mammals and birds, respectively, and represent threshold levels of Hg in fish tissue above which some piscivorous wildlife could start to incur risk [64]. Similar benchmarks have been proposed by Eisler [65], who recommends less than 100 ng/g of total Hg in food items as a protective level for sensitive species of birds and mammals that regularly consume fish and aquatic invertebrates. Fish from Caddo Lake, especially those from the wetland habitat, had mean Hg concentrations high enough to pose a risk to some piscivorous wildlife. Six of the eight species collected from the wetland had mean Hg concentrations above the U.S. EPA critical value for birds. Previous studies at Caddo Lake have found that piscivorous snakes captured near wetland habitats had Hg concentrations as high as 8,610 ng/g wet weight [66], confirming that Hg is bioaccumulating to high levels in piscivorous wildlife. Caddo Lake wildlife should be monitored to determine if they are being negatively impacted by Hg contamination.

CONCLUSION

Our present results help to clarify the relationship between ecological variables and Hg concentration in fish and can be used by researchers as well as public and environmental health officials when designing Hg monitoring studies. Trophic position is an important predictor of Hg concentration in fish between species, and the rate of biomagnification (i.e., the per-trophic-level increase in Hg concentration) is similar in diverse ecosystems and regions [44]. Assessing trophic position, however, likely will be of little utility in studies focused on a single species of fish unless individuals undergo substantial ontogentic diet shifts. Fish size and age are the most appropriate variables for assessing within-species variation in tissue Hg concentration. Studies in other shallow ecosystems are needed, but the present results could indicate that $\delta^{13}C$ values have limited utility as a predictor of Hg concentration in fish from shallow lakes or reservoirs. Finally, the habitat or locations within lakes from which fish are collected may be more important for predicting Hg concentrations in fish than has been appreciated. Habitat-specific differences in Hg accumulation is significant, because the risk posed to human and wildlife health by elevated concentrations of Hg could be underestimated in ecosystems where habitat-specific differences in Hg accumulation are not properly assessed.

SUPPORTING INFORMATION

Table S1. Unadjusted mean (±95% confidence interval) $\delta^{13}C$ and $\delta^{15}N$ values for fish and invertebrates collected from forested-wetland and open-water habitats.

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