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Reservoirs and water management influence fish mercury concentrations in the western United States and Canada

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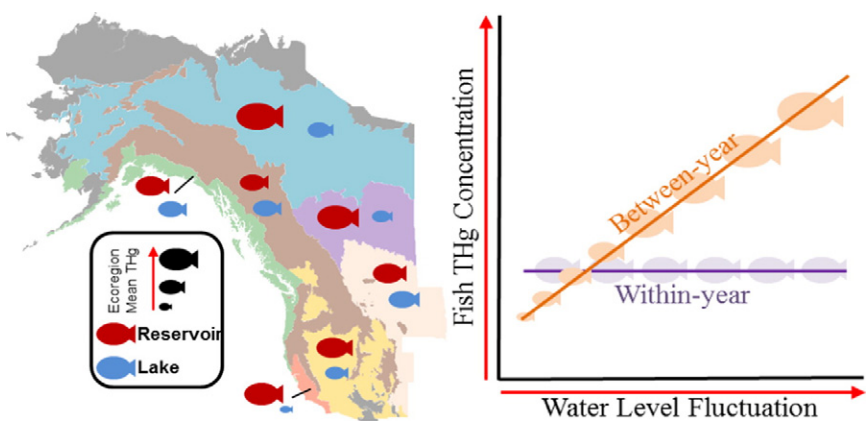
HIGHLIGHTS

- Fish Hg concentrations were compared in lakes and reservoirs of western N. America.
- Hg concentrations were higher in reservoirs than lakes in some ecoregions.
- Peak Hg concentrations occurred in 3 year old reservoirs and then declined.
- Timing of minimum storage and between-year fluctuation effected Hg concentrations.
- Water management practices influence Hg bioaccumulation in many reservoirs.

GRAPHICAL ABSTRACT



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ABSTRACT

Anthropogenic manipulation of aquatic habitats can profoundly alter mercury (Hg) cycling and bioaccumulation. The impoundment of fluvial systems is among the most common habitat manipulations and is known to increase fish Hg concentrations immediately following impoundment. However, it is not well understood how Hg concentrations differ between reservoirs and lakes at large spatial and temporal scales or how reservoir management influences fish Hg concentrations. This study evaluated total Hg (THg) concentrations in 64,386 fish from 883 reservoirs and 1387 lakes, across the western United States and Canada, to assess differences between reservoirs and lakes, as well as the influence of reservoir management on fish THg concentrations. Fish THg concentrations were 1.4-fold higher in reservoirs (0.13 ± 0.011 μg/g wet weight ± standard error) than lakes (0.09 ± 0.006), though this difference varied among ecoregions. Fish THg concentrations were 1.5- to 2.6-fold higher in reservoirs than lakes of the North American Deserts, Northern Forests, and Mediterranean California ecoregions, but did not differ between reservoirs and lakes in four other ecoregions. Fish THg concentrations peaked in three-year-old reservoirs then rapidly declined in 4–12 year old reservoirs. Water management was particularly important in influencing fish THg concentrations, which were up to 11-times higher in reservoirs with minimum water storage occurring in May, June, or July compared to reservoirs with minimum storage occurring in other months.

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Between-year changes in maximum water storage strongly influenced fish THg concentrations, but within-year fluctuations in water levels did not influence fish THg concentrations. Specifically, fish THg concentrations increased up to 3.2-fold over the range of between-year changes in maximum water storage in all ecoregions except Mediterranean California. These data highlight the role of reservoir creation and management in influencing fish THg concentrations and suggest that water management may provide an effective means of mitigating Hg bioaccumulation in some reservoirs.

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1. Introduction

Mercury (Hg) contamination is globally ubiquitous in aquatic ecosystems (Driscoll et al., 2013). Western North America presents a particularly heterogeneous landscape of diverse Hg sources from legacy mining and atmospheric deposition, coupled with extreme gradients in habitats and environmental conditions (Eagles-Smith et al., 2016b this issue). The aridity gradient in western North America has fostered widespread human modification of aquatic environments, which influence Hg risk because of associated alterations to complex biogeochemical and ecological processes that regulate the production and bioaccumulation of methylmercury (MeHg), the most common and toxic form of Hg in biota (Clarkson and Magos, 2006). This is important because MeHg production can influence Hg concentrations in biota more than total inorganic Hg inputs in some systems (Benoit et al., 2003; Suchanek et al., 2008; Wiener et al., 1990). Reservoir creation, and associated hydrologic management, are among the most widespread anthropogenic modifications of aquatic ecosystems, and may influence Hg cycling and MeHg bioaccumulation at a global scale (Rosenberg et al., 2000).

The modern development of western North America was made possible by impounding waterways to create reservoirs for water storage, irrigation, flood control, and hydropower (Travis, 2003). There are nearly 23,000 dams in the western United States (Graf, 1999) that are capable of storing almost 6 times the mean annual runoff of the region (Sabo et al., 2012; Sabo et al., 2010). Although dams provide many social and economic benefits to society, impounding natural waters fundamentally alters the functioning of riverine ecosystems. Impoundment changes geomorphological processes, both in the inundated reach and downstream (Kingsford, 2000; Sabo et al., 2012); biogeochemical processes such as organic carbon transport, nutrient inputs, and oxygenation (Friedl and Wüest, 2002); and ecological processes such as community composition, ecosystem productivity, and bioenergetics (Bunn and Arthington, 2002; Ligon et al., 1995). Thus, the semi-fluvial nature of reservoirs coupled with their manipulated hydrologic cycles make reservoirs unique from most non-impounded lakes (Friedl and Wüest, 2002; Hall et al., 2005). All of these processes play fundamental roles in the distribution, methylation, and bioaccumulation of Hg (Hall et al., 2005), and thus may result in differences in Hg cycling between reservoirs and non-impounded lakes.

The influence of reservoir creation on mercury cycling, frequently referred to as the 'reservoir effect' (Bodaly et al., 1984; Jackson, 1988; Stewart et al., 2008), is a well-documented phenomenon (Bodaly et al., 1984; Hall et al., 2005; Hecky et al., 1991; Lodenius et al., 1983; St. Louis et al., 2004; Verta et al., 1986) resulting in elevated MeHg concentrations in biota following reservoir impoundment. These increases in biotic MeHg concentrations have largely been attributed to enhanced microbial methylation of inorganic Hg resulting from inundation of terrestrial organic matter and favorable redox conditions in flooded soils (Bodaly et al., 1984; Friedl and Wüest, 2002; Hall et al., 2005; Lucotte et al., 1999). Thus, factors that influence the quantity and quality of organic matter or the prevalence of anoxia result in substantial variation in the magnitude and duration of increases in MeHg concentrations after reservoir creation (Hall et al., 2005; Johnston et al., 1991; Larssen, 2010; Verta et al., 1986). Even after the initial pulse of MeHg production associated with reservoir creation, the structure and management of reservoirs continue to influence Hg cycling (Caldwell et al., 2000; Eckley et al., 2015; Hall et al., 2005). Despite the established influence of reservoir creation on fish MeHg concentrations, relatively little is known about how reservoir management influences fish Hg concentrations, nor how these contamination levels differ from more natural lake ecosystems across large landscapes.

The hydrologic cycles of reservoirs are highly managed and dependent on the purpose of each reservoir. As a result, many reservoirs experience substantial water level fluctuations, with widely different timing and duration (Grigg, 1996; Poff and Hart, 2002). For example, reservoirs managed for flood control are often maintained at low water levels, but experience large fluctuations during precipitation events, whereas reservoirs managed for other purposes may have more stable water levels (Eckley et al., 2015; Poff and Hart, 2002). This is important, because repeated wetting and drying of sediments associated with water level management may further stimulate methylation of inorganic Hg (Eckley et al., 2015; Snodgrass et al., 2000). However, the magnitude of this effect is likely dependent upon the extent, timing, and duration of water level fluctuations. Three sediment regions are associated with water level fluctuations; 1) permanently inundated sediments, 2) sediments exposed to the atmosphere for relatively short (≤1 year) periods, and 3) sediments exposed for longer (>1 year) periods, but still periodically inundated. Exposure of sediments for longer periods may be especially important for MeHg production due to associated increases in sediment re-oxidation and colonization by early successional vegetation, which stimulate MeHg production upon re-inundation (Larson et al., 2014; Selch et al., 2007; Snodgrass et al., 2000; Sorensen et al., 2005). Further, identifying the effects of between- versus within-year water level fluctuations on fish THg concentrations may be particularly valuable in understanding, and adaptively managing, the impacts of extended droughts, which have become increasingly common in western North America.

Broad, landscape-scale studies that compare Hg concentrations in fish from reservoirs to those from non-impounded lakes are limited due to the difficulty of comparing impoundments in differing stages of development to natural lakes (Depew et al., 2013a; Depew et al., 2013b; but see Kamman et al., 2005; and Monson et al., 2011). Further, it is unclear how contemporary water management influences Hg concentrations in reservoirs. Thus, an extensive dataset of Hg concentrations in fish from reservoirs and non-impounded lakes across the western United States and Canada was compiled to test whether Hg concentrations in fish differed between reservoirs and non-impounded lakes across this broad geographical area. Additionally, the influence of reservoir age and water management practices on fish Hg concentrations was assessed.

2. Materials and methods

2.1. Mercury data compilation

Fish total mercury (THg) concentration data from reservoirs and lakes were compiled from a variety of existing sources including: monitoring programs, non-routine surveys, and government and academic research projects occurring in the western United States and Canada (Eagles-Smith et al., 2016a; Fig. S1). The resulting dataset included data collected with a variety of analytical methods during a period of over four decades (1969–2011). Although analytical technology has

developed considerably over this period, data were not excluded based on analytical method or analysis date since these changes impact analytical precision rather than accuracy. Data were screened to remove duplicate records, georeferenced, and all collection locations from a waterbody were aggregated into a single point at the centroid of each lake or reservoir (see Eagles-Smith et al., 2016a this issue for details). Each waterbody was also classified into Level I ecoregions (Omernik and Griffith, 2014; www.epa.gov/wed/pages/ecoregions.html; Fig. S1). Fish THg concentrations were standardized to μg/g, and all concentrations converted to wet weight THg concentrations (μg/g ww) either using the sample-specific moisture content (when reported) or the mean moisture content of fish (76%) across all available samples when moisture content was not reported. Whole body THg concentrations were converted to equivalent THg concentrations for skinless, boneless fillets by dividing by 0.74, the average ratio of whole body to muscle THg concentrations for individual fish (Bevelhimer et al., 1997; Boalt et al., 2014; Goldstein et al., 1996). All fish lengths were standardized to fork length (cm) using species specific fork length-to-total length or fork length-to-standard length ratios reported in FishBase (Froese and Pauly, 2003). Any records that had ambiguous locations, tissue types, or length types were removed prior to analysis.

To account for the substantial range of fish sizes represented in the dataset, individual fish THg concentrations were size adjusted to the concentration at the median lengths of each species, except when a likelihood ratio test suggested that length was not correlated with THg concentrations in a particular species. To facilitate size adjustment in underrepresented species, related species with similar ecological and physiological characteristics were grouped (Table S1). For each species group, THg concentrations of individual fish were predicted at the median length for that species (i.e., not the median length of the species group; Table S1) using linear mixed-effect models (e.g., one for each species group) with fork length as a fixed covariate and waterbody, species, and a species × fork length interaction as random effects. These models were developed with a larger fish Hg dataset including fish from all habitats in the western United States and Canada (i.e., not just lakes and reservoirs; Eagles-Smith et al., 2016a this issue). The residuals were then added back to the median-length predicted THg concentrations to calculate the THg concentrations for individual fish.

2.2. Reservoir data compilation

Waterbodies were identified as lakes or reservoirs and wetlands, streams, rivers, and canals excluded, using the National Hydrology Dataset (NHD; http://nhd.usgs.gov/data.html) in the U.S. and the National Hydro Network (NHN; http://www.geobase.ca/geobase/en/data/nhn/description.html) in Canada. Waterbodies with known point-source industrial impacts (e.g., chlor-alkali facilities) were not included in the dataset. The U.S. Army Corps of Engineers National Inventory of Dams (NID; http://nid.usace.army.mil), Atlas of Canada dams data (http://www.nrcan.gc.ca/earth-sciences/geography/atlas-canada), NHN Manmade Features data, and the Global Reservoir and dam database (GRanD; http://www.gwsp.org/products/grand-database.html) were used to further distinguish impounded from non-impounded waterbodies. Any waterbody with an inventoried dam was designated a reservoir, whereas lentic waterbodies without an inventoried dam were designated as non-impounded lakes (hereafter, lakes). Lakes with low weirs that passively stabilize natural water levels were not considered impounded.

To examine the influence of water management, specifically the magnitude and seasonality of water level fluctuations in reservoirs, in-situ reservoir storage (volume) data was obtained for a subset of reservoirs from the U.S. Bureau of Reclamation (BOR), Army Corps of Engineers (ACOE), and California Data Exchange Center (CDEC; Table 1). Storage is monitored continuously in each reservoir using sensors that convert real-time water level measurements to volume using the elevation-volume curves established for each reservoir (US Bureau of Reclamation, 2001). For each reservoir, monthly mean reservoir storage was extracted for all water years between 1964 (or earliest record) and 2015, and standardized to cubic kilometers (km^3) units. Because the collection intervals (i.e., every 15 min, 1 h, 6 h, or 24 h), completeness, and quality of these data varied considerably among data sources and waterbodies, a series of filters was applied to all of the source data prior to analysis. First, any storage values that were outside of an operational range (i.e., the minimum and maximum capacities of the reservoir) were flagged for further examination. The majority of these cases were sensor failures indicated by numerical error codes, obvious decimal place errors, or obvious errors in units because they were different than the remaining data for that waterbody. If a value was missing, or the source of the error could not be positively identified, the datum was excluded. In some cases, the resulting data gaps could be filled by referencing alternative sensors from the same reservoir. Finally, the completeness of each record was assessed and water years missing >15% of records were excluded.

Table 1
Data sources for reservoir fluctuation data, number of reservoirs with fluctuation data, and years utilized in fluctuation analysis.

Data source	N	# sites	Years
Army Corp of Engineers - Northwest Division[a]	1127	11	1969–2011
California Data Exchange Center[b]	2005	113	1965–2011
U.S. Bureau of Reclamation			
Great Plains Region[c]	999	28	1967–2012
Pacific Northwest Region[d]	334	25	1965–2011
Upper Colorado Region[e]	419	12	1983–2011

[a] http://www.nwd-wc.usace.army.mil/cgi-bin/dataquery.pl.
[b] http://cdec.water.ca.gov/reservoir.html.
[c] http://www.usbr.gov/gp/hydromet.
[d] http://www.usbr.gov/gp/hydromet.
[e] http://www.usbr.gov/rsvrWater/faces/rvrOSMP.xhtm.

To examine the potential effects of timing of water level fluctuations on fish THg concentrations, reservoirs were classified based upon the month in which they typically reached their annual minimum storage during the five-years prior to each fish collection event (Fig. 1a). Water level fluctuations were also calculated for each water year in which at least three fish were sampled from a reservoir and sufficient storage data existed. Within-year water storage fluctuations were calculated as the difference between the minimum and maximum monthly storage levels within a water year (Fig. 1b) and converted to estimates of the proportional within-year change in water storage by normalizing with the minimum monthly storage for the year. This within-year change in reservoir water storage represents the relative area of sediments that have been exposed for less than one year, and are inundated upon reservoir filling. Between-year change in maximum water storage was also calculated as a proxy for the relative area of sediment that was re-inundated after being exposed for more than one year. Between-year change in reservoir water storage was calculated as the difference between maximum water storage in the sampling year and the previous year (Fig. 1c), converted to proportional estimates of between-year change in water storage by normalizing with the maximum storage of the previous year. Both within- and between-year fluctuations in water storage levels were averaged over the five-year period prior to fish collections except in a few cases where a three- or four-year period was used instead due to incomplete water level data for some waterbodies.

2.3. Statistical analysis

The programs JMP® (version 12.0.1; SAS Institute Inc.) and R (version 3.1.0; www.r-project.org) were used for statistical analysis of size adjusted and natural-log transformed fish THg concentrations (μg/g ww). Unless otherwise specified, results are presented as back-transformed least-squares means with standard errors estimated using the delta method (Williams et al., 2002).

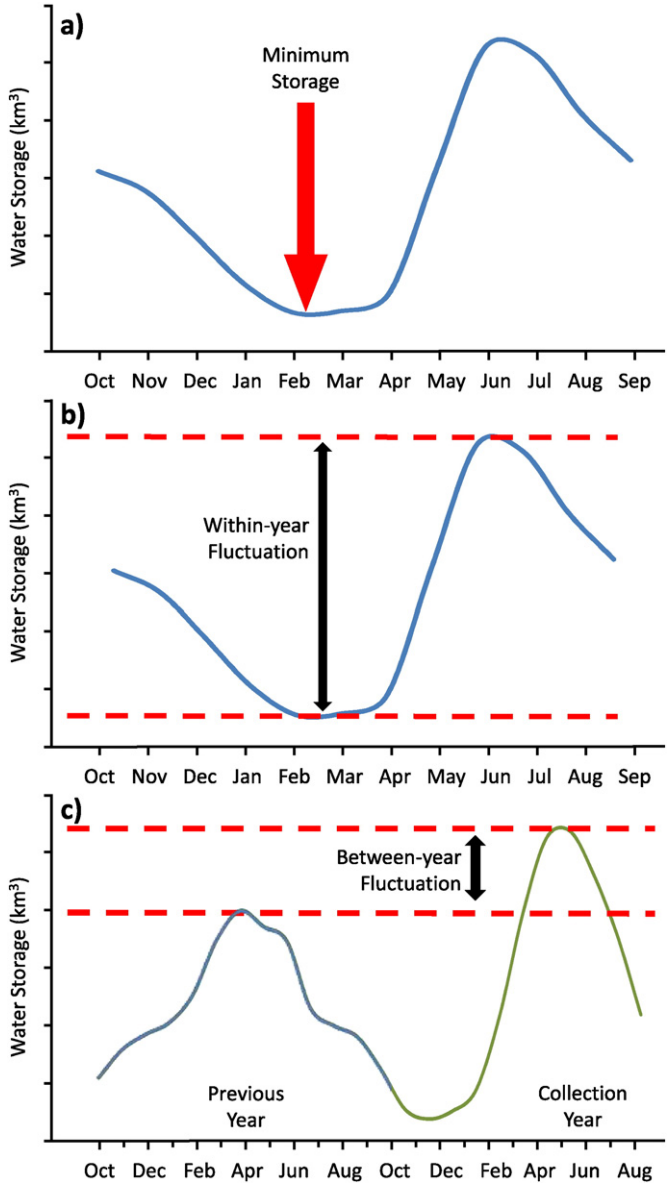

Fig. 1. Conceptual diagram detailing the calculation of three water management parameters: a) timing of minimum water storage; b) within-year change in water storage; and c) between-year change in water storage. All three parameters were averaged over the five-years preceding each fish collection.

Differences in fish THg concentrations between lakes and reservoirs were assessed using a linear mixed-effects model with habitat (reservoir or lake) and ecoregion as fixed effects; waterbody, species, and sampling year as random effects; and a habitat × ecoregion interaction. This model was contrasted with three similar models for subsets of the data to assess potential biases due to 1) the inclusion of rare taxa, 2) variation in background contamination, and 3) the influence of waterbody size. The first alternative was the same as the selected model but only included data for species with data from at least 15 sites. The second alternative included soil THg concentrations interpolated from point data (Smith et al., 2013) as a covariate. The third alternative analysis included waterbody surface area as a covariate and an interaction between surface area and habitat. In all three alternatives, the results were similar to those of the simpler model using the full dataset (Table S2); therefore, the full dataset was used and neither soil THg nor waterbody surface area was included as a covariate.

The influence of reservoir age on fish THg concentrations was assessed using a linear mixed-effects model that included ecoregion and reservoir age as categorical fixed effects; with waterbody, species, and sampling year as random effects. A segmented regression (Toms and Lesperance, 2003) followed by a Davies test (Piepho and Ogutu, 2003) was also employed to identify potential breakpoints in the relationship between fish THg concentrations and reservoir age after accounting for the effects of ecoregion, waterbody, species, and sampling year.

A subset of the data was used to examine the effects of water level management on fish THg concentrations in reservoirs. First, data were analyzed in a single linear mixed-effects model with ecoregion and month the minimum storage level occurred as fixed effects; within- and between-annual changes in water storage as covariates; and waterbody and species as random effects. The effects of water management could differ among ecoregions, but interactions could not be included in the above global model, because not all months were represented as water storage minimums in each ecoregion. Therefore, ecoregion-specific models were subsequently used to examine the influence of water level management on fish THg concentrations in individual ecoregions.

3. Results and discussion

3.1. Reservoirs versus non-impounded lakes

A total of 64,386 fish THg concentrations were complied, representing 157 species from 883 reservoirs and 1387 lakes throughout the western United States and Canada (Table 2). Across all ecoregions, species, waterbodies, years, and fish sizes, geometric mean THg concentrations (μg/g ww ± standard error) in skinless boneless fish fillet was 0.23 ± 0.001 (n = 27,007) in reservoirs compared to 0.17 ± 0.001 in lakes (n = 37,379). Records lacking length data or from waterbodies with total sample sizes of less than three individuals (n = 4534) were excluded from subsequent analyses.

After accounting for the influence of species, waterbody, year, and ecoregion, size-adjusted least squares mean fish THg concentrations were 44% higher in reservoirs than lakes (reservoirs = 0.13 ± 0.011, lakes = 0.09 ± 0.006, $F_{1,2146} = 22.59$, $P < 0.001$; Fig. 2); however, the significant interaction between ecoregion and habitat ($F_{6,2917} = 9.23$, $P < 0.001$) indicated that the difference between lakes and reservoirs was not consistent among ecoregions. In individual ecoregions, fish THg concentrations (μg/g ww ± standard error) differed between reservoirs and lakes in Mediterranean California (reservoirs = 0.15 ± 0.013, lakes = 0.07 ± 0.008, $P < 0.001$), North American Deserts (reservoirs = 0.14 ± 0.011, lakes = 0.09 ± 0.009, $P < 0.001$), and Northern Forests (reservoirs = 0.16 ± 0.059, lakes = 0.08 ± 0.006, $P = 0.003$) ecoregions (Fig. 2). Least squares mean fish THg concentrations also tended to be higher in reservoirs than in lakes from Taiga ecoregion (reservoirs = 0.18 ± 0.067, lakes = 0.10 ± 0.009; Fig. 2), though the difference was not statistically significant ($P = 0.14$). Fish THg concentrations were similar between reservoirs and lakes of the Great Plains

Table 2
Number of sites and sample sizes for fish from reservoirs and lakes in 10 ecoregions in the western United States and Canada.

Ecoregion	Reservoirs		Lakes	
	# sites	N	# sites	N
Great Plains	240	11,398	149	4632
Marine West Coast Forest	17	1198	72	986
Mediterranean California	139	3115	59	679
North American Deserts	194	4999	84	606
Northern Forests	6	1059	567	19,259
Northwestern Forested Mountains	251	4288	280	3804
Southern Semiarid Highlands	6	213	1	3
Taiga	3	291	139	6579
Temperate Sierras	27	446	3	13
Tundra	0	0	33	818

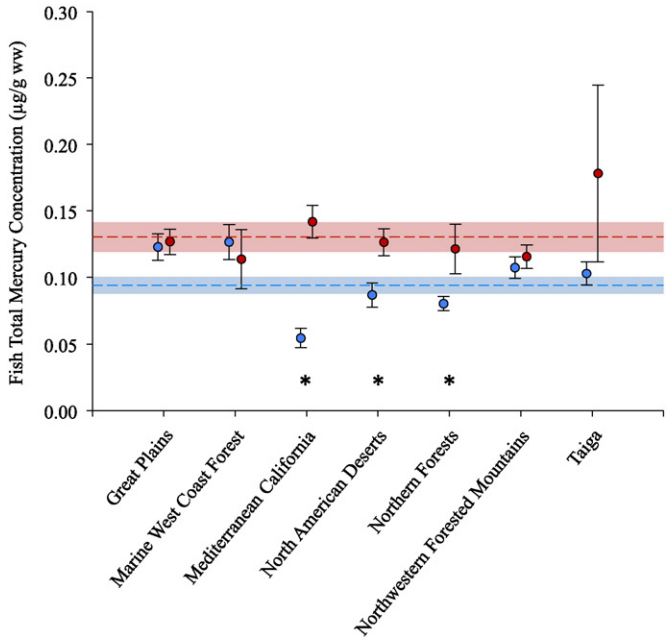

Fig. 2. Least squares mean total mercury concentrations (µg/g ww ± standard error) in size-standardized fish from reservoirs (red-darker grey) and non-impounded lakes (blue) in the western United States and Canada. Points are least squares means for individual ecoregions whereas dashed lines are the global least squares means (shaded area is standard error) across all ecoregions. Least squares mean account for the effects of ecoregion (global least squares means only), species, waterbody, and sampling year. Ecoregions where reservoirs and non-impounded lakes were significantly different ($P < 0.05$) are marked with an asterisk.

(reservoirs = 0.13 ± 0.009, lakes = 0.12 ± 0.010, $P = 0.62$), Marine West Coast Forest (lake = 0.13 ± 0.013, reservoir = 0.11 ± 0.022, $P = 0.60$), and Northwestern Forested Mountains (lake = 0.11 ± 0.008, reservoir = 0.12 ± 0.009, $P = 0.24$) ecoregions (Fig. 2).

Fish THg concentrations were 1.5, 1.6, and 2.6-fold higher in reservoirs than non-impounded lakes in the North American Deserts, Northern Forests, and Mediterranean California ecoregions, respectively. Similar differences (1.7-fold) were observed between reservoirs and lakes in the Taiga ecoregion though these differences were not significant, likely due to the small number of reservoirs with data from this ecoregion (Table 2). These differences are within the range of those found in other comparisons of reservoirs and lakes in several areas. For example, fish THg concentrations from eight recently flooded reservoirs in northern Manitoba were 1.6- to 8.9-fold higher than from nearby lakes (Bodaly et al., 1984; Bodaly et al., 2007), and fish from 11 Finnish reservoirs had THg concentrations 1.4- to 3.5-fold higher than those in fish from reference lakes (Lodenius et al., 1983). Although the differences observed in the current study are on the lower end of these ranges, our analysis included reservoirs ranging in age from <1 year to nearly 160 years old, whereas the majority of reservoirs in the prior studies were less than two decades old. This difference in reservoir age may be particularly important considering the temporal dynamics of fish THg concentrations associated with reservoir creation and ageing (discussed further below). In fact, fish THg concentrations from reservoirs <12 years old were significantly higher than concentrations in lakes for all ecoregions ($F_{1,1107} = 25.22$, $P < 0.001$).

These differences in fish Hg concentrations between habitats likely translate into increased risk to fish, wildlife, and human consumers utilizing fish from reservoirs versus lakes. Across all ecoregions, 44% of individual fish THg concentrations from reservoirs exceeded the US EPA benchmark for safe consumption (0.3 µg/g ww) compared to 31% for non-impounded lakes. However, 50% of fish from reservoirs in the North American Deserts, Northern Forests, and Mediterranean California ecoregions exceeded the EPA benchmark compared to only 20% of fish from non-impounded lakes in these regions. This is similar to findings from Finland where 66% of fish sampled from reservoirs exceeded the Finnish consumption benchmark (0.5 µg/g ww) compared to 35% of fish from natural lakes (Porvari, 1998).

This is the first study with sufficient spatial breadth to compare fish THg concentrations from reservoirs and lakes across multiple ecoregions. The factors responsible for the variation in the differences between reservoirs and lakes among ecoregions are unclear, but it is unlikely that they result from inherent bias in the dataset. Despite variation in the fish species represented in each ecoregion, foraging guilds and average trophic position of fishes were similar among reservoirs and lakes both within and among ecoregions (guild and trophic position of each species were based on ecological data reported in FishBase; Froese and Pauly, 2003) (Table S3). Similarly, reservoir ages did not differ among ecoregions where fish THg concentrations were higher in reservoirs than in lakes (median = 42 years) and ecoregions with no difference in fish THg concentrations between habitats (median = 43 years). Rather, regional variation in Hg deposition (Weiss-Penzias et al., 2016), sedimentary MeHg concentrations and loading (Fleck et al., this issue), or other biogeochemical conditions, coupled with differences in climate, reservoir management and basin morphology, likely contribute to the observed variation among ecoregions. Although several studies have examined drivers of differences between boreal reservoirs and lakes (French et al., 1998; Jackson, 1988; Johnston et al., 1991; Verta et al., 1986), these data suggest that quantitative comparisons of drivers among regions is a valuable direction for future research.

3.2. Reservoir age influences on fish mercury concentrations

Changes in fish THg concentrations following reservoir impoundment is a source of variation among reservoirs that has received considerable previous attention, though typically only in relatively young reservoirs. Reservoirs in this study ranged in age from 0 to 157 years old (post-impoundment) at the time of fish sampling, with some reservoirs completed as recently as 2010. Sampling events were relatively well distributed among reservoirs of varying ages, with the exception of the oldest reservoirs, which tended to be sampled more recently (Table S4). After statistically accounting for the effects of waterbody, species, and sampling year, there was a substantial effect of reservoir age on size-adjusted fish THg concentrations ($F_{1231,12771} = 14.51$, $P < 0.001$; Fig. 3). Segmented regression identified two breakpoints in the relationship between fish THg concentrations and reservoir age, the first occurred at 3.04 ± 0.71 years and the second at 12.48 ± 1.33 years (Davies-test, k = 1000, $P < 0.001$; Fig. 3). Least squares mean THg concentrations in fish increased from 0.27 ± 0.039 µg/g ww in reservoirs <1 year old to 0.43 ± 0.061 µg/g ww in 3 year old reservoirs. Fish THg concentrations in 12 year old reservoirs were similar to those in newly formed (<1 year old) reservoirs and continued to decline slightly with reservoir age thereafter (Fig. 3).

These data suggest that fish THg concentrations change dramatically in the decade following reservoir creation. The breakpoints in fish THg trends are consistent with those reported in previous studies of fish THg concentrations from newly formed reservoirs. Maximum THg concentrations in fish from eight Manitoban reservoirs sampled within 32 years of impoundment generally occurred between 2 and 8 years following impoundment (Bodaly et al., 2007). Similarly, fish THg concentrations peaked 3-years after impoundment in Finnish reservoirs (Porvari, 1998), within 6 years for most species in Smallwood Reservoir, Labrador (Anderson et al., 1995), and 5–13 years after impoundment in reservoirs of northern Quebec (Schetagne and Verdon, 1999). In these studies, fish THg concentrations from most species and reservoirs returned to background levels (i.e., within the range of concentrations observed from pre-impoundment or non-impounded lakes) within 10–25 years following impoundment (Anderson et al., 1995; Bodaly et al., 2007; Porvari, 1998; Schetagne and Verdon, 1999). However, some reservoirs in each study had not reached background

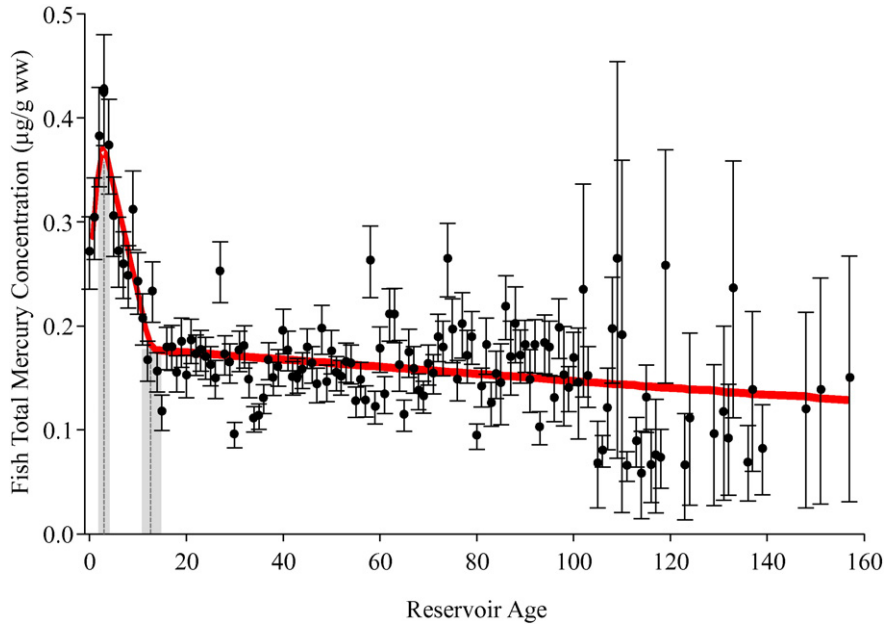

Fig. 3. Least squares mean total mercury concentrations (µg/g ww ± standard error) in size-standardized fish from reservoirs across western North America. Least squares mean account for the effects of ecoregion, waterbody, species, and sampling year. Vertical grey dashed lines and shaded regions indicate estimated breakpoints (±standard error) from segmented linear regression (solid line) on fish mercury concentration when accounting for the effects of ecoregion, waterbody, species, and sampling year.

concentrations after 30 or more years, and in some reservoirs in Newfoundland have remained elevated for at least 60 years following impoundment (French et al., 1998). In the current study, fish THg concentrations in reservoirs did not generally approach the global least squares mean of non-impounded lakes (Fig. 2) for at least a century following impoundment (Fig. 3). Thus, although the initial changes in fish THg concentrations following reservoir impoundment are an important characteristic of Hg cycling in reservoirs, these data suggest that fish THg remain elevated even in long-established reservoirs.

3.3. Water management influences on fish mercury concentrations

Water storage fluctuation data and fish THg concentrations from for 189 reservoirs, representing 355 sampling events, were analyzed to better understand the processes associated with increased fish THg concentrations in reservoirs relative to lakes. Specifically, a linear mixed-effects model that accounted for variation due to ecoregion, waterbody, species, and year was used to determine whether fish THg concentrations were affected by the timing of drawdowns, or within- and between-year water storage fluctuations. Across all ecoregions, the month in which reservoirs reached minimum capacity was an important determinant of fish THg concentrations ($F_{11,1049} = 8.49$, $P < 0.001$; Fig. S2a). Reservoirs with minimum water storage levels occurring between April and July had least squares mean fish THg concentrations that were 1.8 to 3.5-fold higher than those with typical minimum water storage levels occurring between August and March (Fig. S2a). Additionally, the between-year change in maximum water storage had a strong impact on fish THg concentrations ($F_{1,2453} = 27.71$, $P < 0.001$; Fig. S2b), whereas within-year changes between minimum and maximum water level were not correlated with fish THg concentrations ($F_{1,691} = 8.49$, $P = 0.26$; Fig. S2c). In fact, predicted fish THg concentrations increased by 3.2-fold over the range of observed between-year change in maximum water storage, but did not vary over the range of within-year changes in water storage.

Whereas the above model accounts for the effect of ecoregion, the model would not converge with interactions between ecoregion and the water management parameters. Therefore, ecoregion-specific models were used to assess whether water level fluctuations affected fish THg concentrations differently among ecoregions. The month in which reservoirs reached minimum water storage was a significant predictor of fish THg concentrations in the Great Plains ($F_{6,40} = 5.53$, $P < 0.001$) and North American Deserts ($F_{10,39} = 3.05$, $P = 0.01$) ecoregions after accounting for the effects of between- and within-year water storage fluctuations, waterbody, and species. In both of these ecoregions, least squares mean THg concentrations were lower in reservoirs with minimum water storage occurring in January or February and higher in reservoirs with minimum water storage occurring during March and April (Fig. 4). In the North American Deserts this trend continued upwards and reservoirs with minimum water storage occurring during July had fish THg concentrations 13.6-fold higher than reservoirs with minimum water storage occurring in January. Fish THg concentrations were 4.6- and 2.9-fold lower in Great Plains and North American Desert reservoirs with minimum water storage occurring in August than in reservoirs with minimum water storage occurring in July (Fig. 4). Least squares mean THg concentrations followed a similar trend in the Northwestern Forested Mountains ecoregion, where fish THg concentrations increased 1.8-fold between reservoirs with minimum water

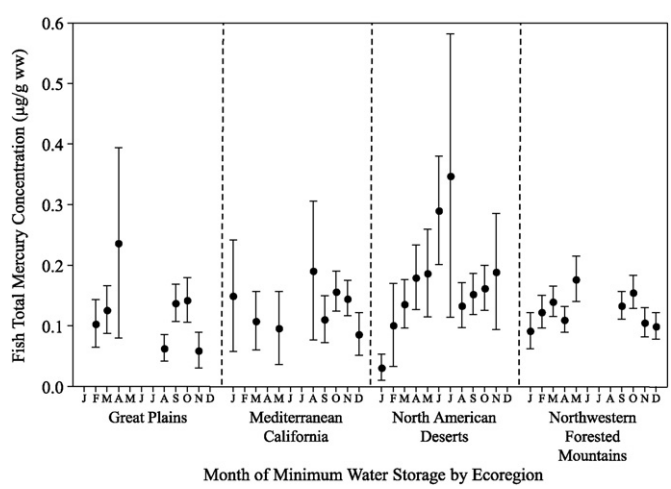

Fig. 4. Least squares mean total mercury (THg) concentrations (µg/g ww ± standard error) in size-standardized fish from reservoirs with minimum water storage levels occurring in different months. Least squares means account for the effects of within- and between-year changes in water storage levels, waterbody, and species.

storage occurring in January and reservoirs with minimum storage occurring in June. Fish THg concentrations then gradually declined in reservoirs with minimum storage levels occurring from September through December ($F_{8,256} = 1.85$, $P = 0.07$; Fig. 4). A possible explanation for this pattern is that exposure of sediments during the spring and early summer growing seasons leads to increased growth of early succession, herbaceous vegetation and subsequent accumulation of labile organic matter, which fuels microbial production upon inundation (Larson et al., 2014). Similar differences have been widely observed among recently impounded reservoirs with varying quantities or quality of flooded organic matter (Johnston et al., 1991; Larssen, 2010; Mailman et al., 2006). The current data suggest that a similar process may also occur over much shorter time frames, when reductions in reservoir water levels expose substrate that allows for plant growth within the reservoir boundaries. In the Mediterranean California ecoregion, fish THg concentrations were not different among reservoirs with water storage minimums that occurred in different months ($F_{7,51} = 0.60$, $P = 0.76$) and there was no apparent pattern in fish THg concentrations among months (Fig. 5). Although months were utilized as the temporal variable in this analysis, it is important to note that individual months do not necessarily correspond to similar conditions in each ecoregion. For example, in much of the Mediterranean California ecoregion maximum growth of terrestrial vegetation on exposed sediments would be expected in the wetter winter months as opposed to summer months. This confounding effect could be avoided by comparing the timing of minimum water levels to remotely sensed phenological indices (Zhang et al., 2003), or preferably to in-situ measurements of vegetative production on exposed sediments. Such studies would provide valuable insights into the mechanisms by which water level fluctuations influence fish THg concentrations.

The effects of within- and between-year changes in water storage within each ecoregion were examined after accounting for the effects of timing of minimum water storage, waterbody, and species. Fish THg concentrations were positively correlated with between-year differences in maximum water storage in the Great Plains ($F_{1,465} = 18.12$, $P < 0.001$), North American Deserts ($F_{1,870} = 32.27$, $P < 0.001$), and Northwestern Forested Mountains ($F_{1,687} = 11.14$, $P < 0.001$) ecoregions, increasing 2.1 to 3.2-fold between the reservoirs with the smallest and largest between-year differences. There was no effect of between-year difference in maximum water storage on fish THg concentrations in the Mediterranean California ecoregion ($F_{1,298} = 0.07$, $P = 0.787$; Fig. 5). In contrast, fish THg concentrations were correlated with within-year changes (annual minimum to annual maximum) in water storage in the Northwestern Forested Mountains ecoregion ($F_{1,278} = 6.99$, $P = 0.01$), where fish THg concentrations increased 2.8-fold over the range of within-year fluctuations, but not in any of the other ecoregions (Great Plains: $F_{1,76} = 0.32$, $P = 0.57$; Mediterranean California: $F_{1,123} = 0.02$, $P = 0.866$; North American Deserts: $F_{1,835} = 0.59$, $P = 0.44$; Fig. 6).

Fish THg concentrations were most often correlated with between-year changes in maximum water storage, but rarely with within-year water storage fluctuations. These results are consistent with previous work that found changes in maximum water levels between years were the strongest predictor of THg concentrations in young-of-year Yellow Perch (*Perca flavescens*) among six different measures of water level fluctuation (Sorensen et al., 2005). Although within-year wetting and drying cycles can facilitate MeHg production in sediments (Benoit et al., 2003; Eckley et al., 2015; Snodgrass et al., 2000), it appears that exposure of sediments for longer time periods further exacerbates this process. Exposure of sediments results in re-oxidation of sediments that increases sediment sulfate and subsequently facilitates methylation by sulfate reducing bacteria (Eckley et al., 2015; Selch et al., 2007). Importantly, sediment sulfate concentrations and subsequent MeHg production are positively correlated with the duration of sediment exposure (Eckley et al., 2015), and are particularly high in sediments that have been exposed for a year or more (Selch et al., 2007). This is an important finding because it suggests that large relative increases in maximum water storage can exacerbate Hg bioaccumulation in western reservoirs. This is particularly true in the more arid North American Deserts and Great Plains ecoregions. The mechanism underlying differences in the effect of water level fluctuations on fish THg concentrations among ecoregions is unclear, but could be due to differences in shoreline characteristics that result in higher sediment exposure during water level fluctuations (Larson et al., 2014) or differences in organic matter inputs (Hall et al., 2005; Larssen, 2010). In particular, fish THg

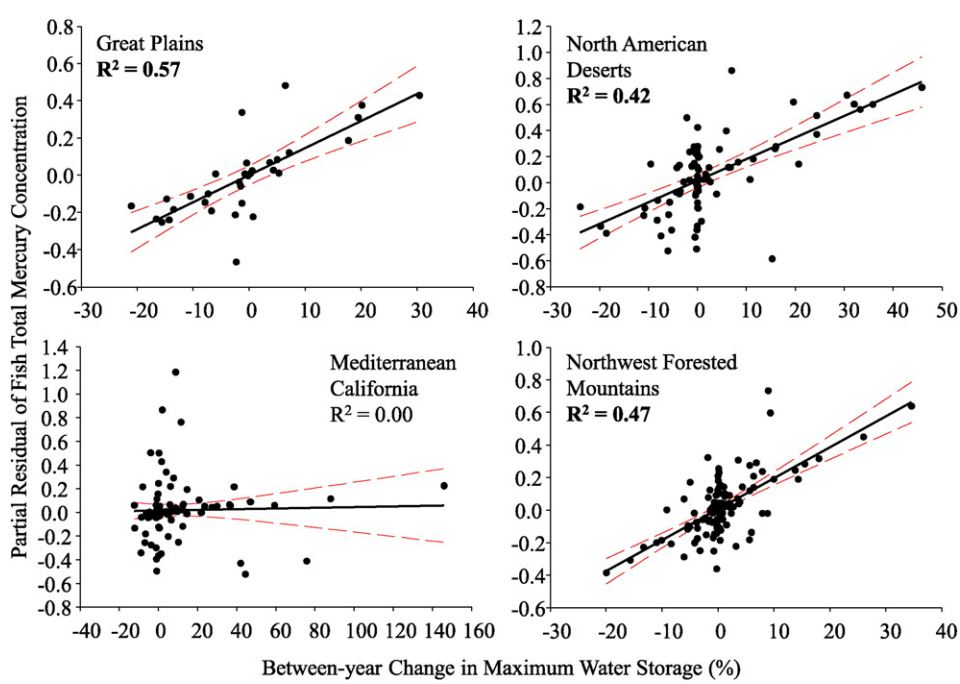

Fig. 5. Partial residual plots depicting the relationships between total mercury concentrations in size-standardized fish and between-year changes in maximum water storage from reservoirs in four ecoregions of the western United States. Partial residuals account for the effects of timing of minimum water storage, within-year changes in water storage, waterbody, and species. R^2 values that are bolded indicate those ecoregions where between-year changes in maximum water storage were correlated with fish THg concentrations.

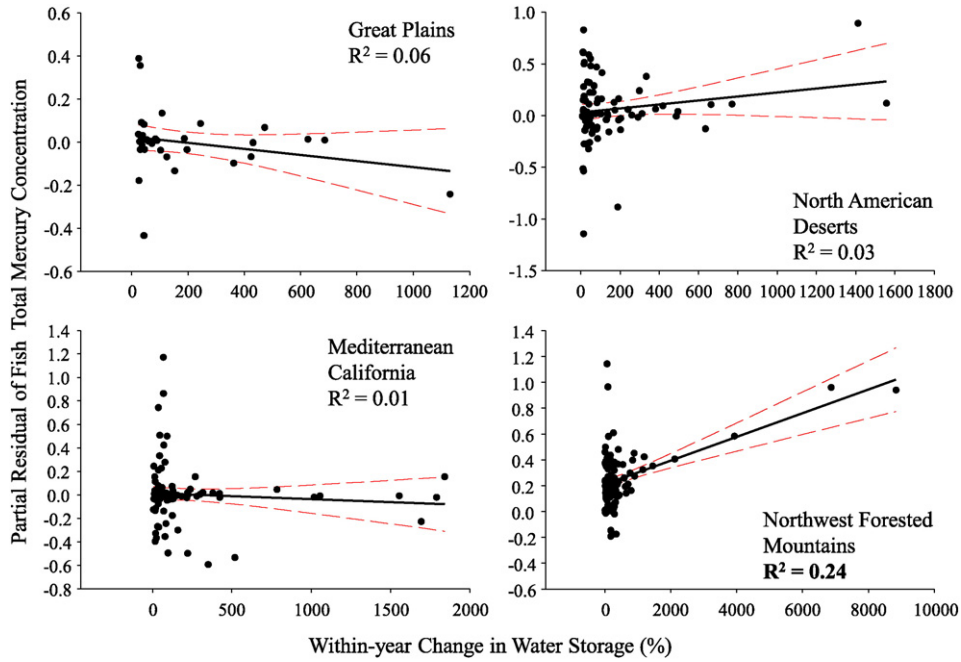

Fig. 6. Partial residual plots depicting the relationships between total mercury concentrations in size-standardized fish and within-year changes in water storage from reservoirs in four ecoregions of the western United States. Partial residuals account for the effects of timing of minimum storage, between-year changes in maximum water storage, site, and species. R^2 values that are bolded indicate those ecoregions where within-year changes were correlated with fish THg concentrations.

concentrations in reservoirs of the Mediterranean California ecoregion appear to be substantially less sensitive to water level fluctuations than reservoirs in other ecoregions. This ecoregion is heavily impacted by legacy mining that has resulted in elevated MeHg concentrations in large proportion of the lowland reservoirs (Alpers et al., 2005; Davis et al., 2010; Stewart et al., 2008). It is possible that such background contamination confounds the effect of water level fluctuations on fish THg concentrations in these systems. Further, the region is subject to one of the most intensive water storage and diversion systems in the world. Because of the high density of reservoirs and prevalence of inter-basin water movements, nearly every reservoir in the region is situated downstream of other reservoirs. Thus, the effects of reservoir water management are likely to be more complex and variably dependent on conditions in reservoirs situated upstream (Bodaly et al., 2007; Johnston et al., 1991; Schetagne et al., 2000). This "downstream effect" can have substantial impacts on fish THg concentrations, with upstream reservoir conditions explaining >75% of the variation in downstream reservoirs, and often more than in-reservoir processes (Johnston et al., 1991). Finally, it cannot be ruled out that the lack of a relationship between water storage fluctuations and fish THg concentrations in the Mediterranean California ecoregion may stem from a bias in our water fluctuation dataset for this ecoregion. Over 90% of the water fluctuation data corresponds to reservoirs where fish were sampled during 2007 or 2008, a period when California was experiencing a severe drought (Christian-Smith et al., 2011).

4. Conclusion

This study provides the largest spatial and temporal evaluation of fish THg concentrations in reservoirs to date. By leveraging such an extensive dataset, it is shown that fish THg concentrations are often higher in reservoirs than non-impounded lakes, and that this relationship varies considerably among ecoregions and age of the reservoir. Importantly, this study did not examine the mechanisms leading to differences among ecoregions, though regional differences in atmospheric Hg deposition (Weiss-Penzias et al., 2016), reservoir characteristics, and water management practices may play a role. Additionally, fish THg concentrations in reservoirs are shown to change dramatically with reservoir age, with the more pronounced increases in fish THg concentrations occurring in the first 3 years after reservoir creation and the larges declines occurring from 3 to 12 years after reservoir impoundment. Thus, management practices that limit the magnitude and duration of this peak, such as pre-flooding biomass reduction and extending filling over longer time-frames (Mailman et al., 2006), may substantially reduce MeHg exposure risk in reservoirs. Of particular importance, these data suggest that in some cases water management may provide a means to reduce MeHg bioaccumulation by manipulating the timing of water storage level minimums. Reducing the amount of sediment exposed (i.e., keeping water levels raised) during the critical spring and summer growing seasons (Jan–Jul) appears to be one mechanism by which fish THg concentrations could be reduced within reservoirs. Whether similar results could be obtained by reducing organic matter accumulation on sediments exposed during this period, or with other treatments, will be of particular interest to managers, especially given increasingly erratic climate patterns which often preclude active management of water levels (Christensen et al., 2004; Pahl-Wostl, 2007). The data also suggests management practices that maintain consistent maximum water levels between years, regardless of the total within-year fluctuation, may be particularly useful for minimizing MeHg bioaccumulation in fish. Although it may be impractical to maintain consistent water levels from one year to the next in the face of increasingly prevalent droughts and unpredictable climate shifts, these results also suggest raising water levels over an extended time period following droughts may have less of an impact than rapid increases in water levels. Future studies examining the biogeochemical and ecological responses to such water management strategies are critical to improving our overall understanding of Hg cycling and reducing Hg contamination in fish and wildlife within these important aquatic habitats.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.03.050.

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Supporting Information

Reservoirs and Water Management Influences on Fish Mercury Concentrations in the Western United States and Canada

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15 pages, 2 figures, 4 tables

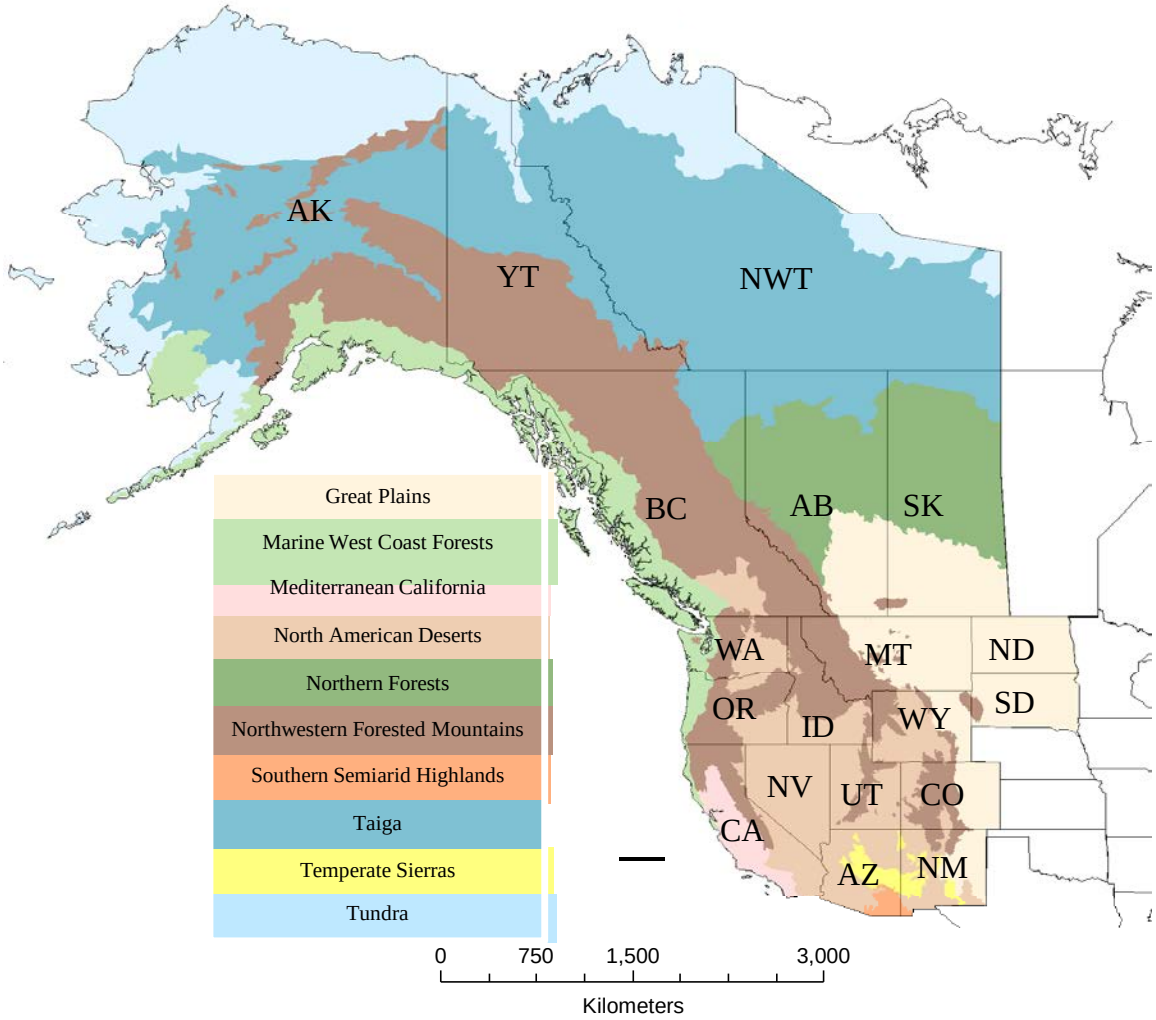

Figure S1: Map of study area depicting states, provinces, and territories included and Level I ecoregions.

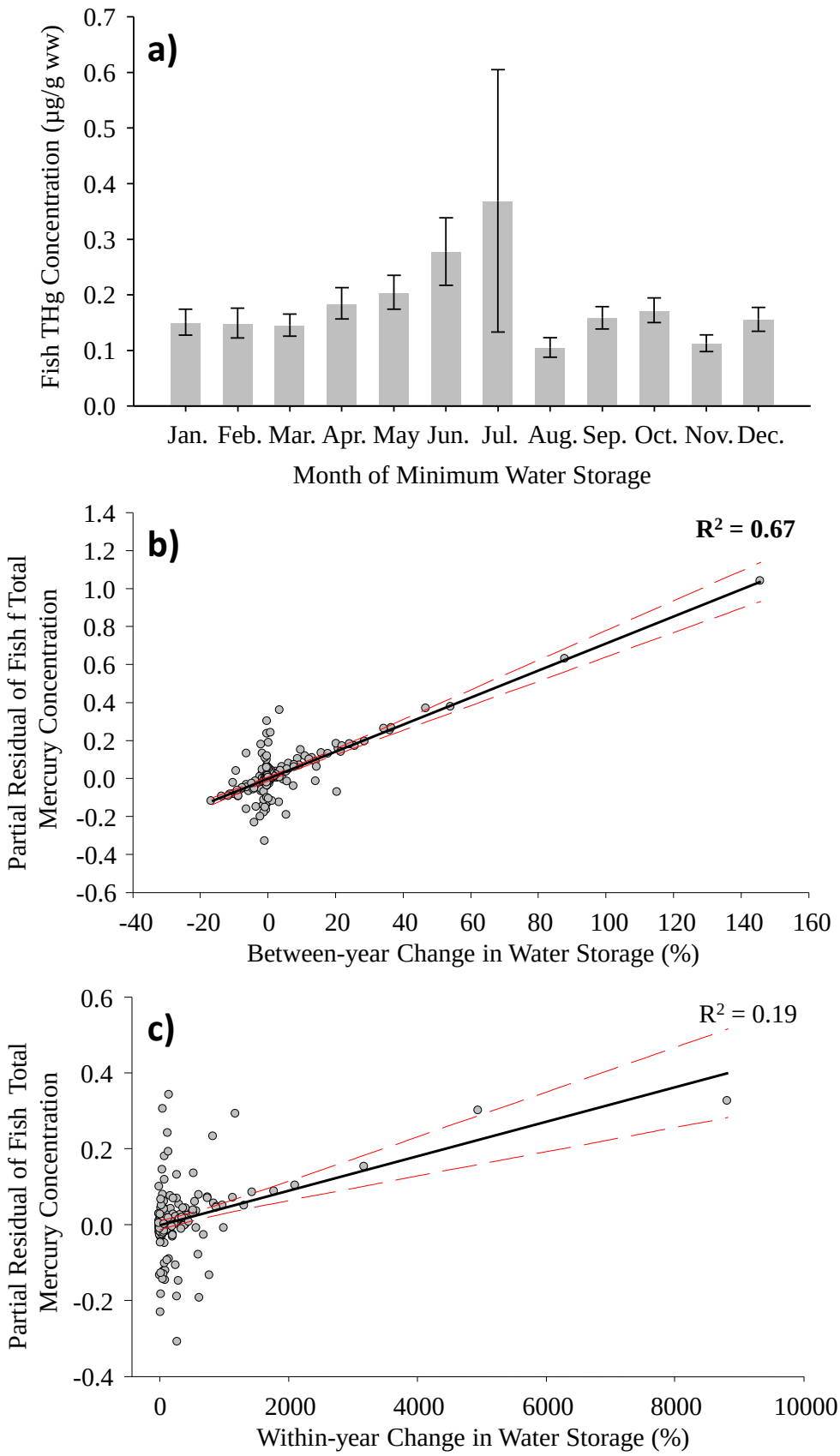
a)
Fish THg Concentration (µg/g ww)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Jan. Feb. Mar. Apr. May Jun. Jul. Aug. Sep. Oct. Nov. Dec.
Month of Minimum Water Storage
b)
R² = 0.67
Partial Residual of Fish f Total Mercury Concentration
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-40 -20 0 20 40 60 80 100 120 140 160
Between-year Change in Water Storage (%)
c)
R² = 0.19
Partial Residual of Fish Total Mercury Concentration
0.6
0.4
0.2
0.0
-0.2
-0.4
0 2000 4000 6000 8000 10000
Within-year Change in Water Storage (%)

Figure S2: Relationships between total mercury (THg) concentrations (µg/g ww ± standard error) in size-standardized fish and reservoir water management parameters across ecoregions of western North America. **a)** Least squares mean fish THg concentrations from reservoirs with minimum water storage occurring in different months. Least squares mean account for the effects of ecoregion, within- and between-year changes in water storage, site, and species. **b)** Partial residual plot depicting the relationship between fish THg concentrations and between-year changes in maximum water storage. Partial residuals account for the effects of ecoregion, timing of minimum storage, within-year changes in water storage, site, and species. **c)** Partial residual plot depicting the relationship between fish THg concentrations and within-year changes in maximum water storage. Partial residuals account for the effects of ecoregion, timing of minimum storage, between-year changes in water storage, site, and species

Table S1: Groups, sample size (N), number of waterbodies, and length for 131 species from reservoirs and lakes in the western United States and Canada. Species with bolded lengths were size corrected with models based on the larger dataset presented in Eagles-Smith et al. (2016).

Species Group	**Common Name** *Scientific Name*	**N**	**# Waterbodies**	**Median Fork Length (cm) (min – max)**
Anadromous salmonids	Arctic Char *Salvelinus alpinus*	16	3	**62.0** **(46.5 – 75.0)**
	Atlantic Salmon *Salmo salar*	3	1	**30.8** **(24.1 – 31.0)**
	Chinook Salmon *Oncorhynchus tshawytscha*	59	7	**65.8** **(30.0 - 101.6)**
	Coho Salmon *O. kisutch*	4	4	**30.0**
	Sockeye Salmon *O. nerka*	30	1	**-**
	steelhead *O. mykiss*	12	1	**79.1** **(60.5 - 90.2)**
	Unspecified salmonid	3	2	**77.5** **(29.1 - 81.2)**
Arctic Grayling	Arctic Grayling *Thymallus arcticus*	167	38	**35.7** **(6.8 – 47.5)**
Silversides	Inland Silversides *Menidia beryllina*	3	2	**-**
Black Bass	Largemouth Bass *Micropterus salmoides*	5086	405	**33.2** **(4.0 – 64.0)**
	Smallmouth Bass *M. dolomieu*	1407	137	**30.0** **(4.4 - 71.4)**
	Spotted Bass *M. punctulatus*	123	10	**27.5** **(12.1 - 45.9)**
	Unspecified black bass *Micropterus* spp.	51	2	**31.9** **(25.1 – 36.0)**
Burbot	Burbot *Lota lota*	737	90	**60.1** **(12.4 - 88.9)**
Carp	Common Carp *Cyprinus carpio*	1137	250	**45.7** **(2.9 - 75.8)**
	Goldfish *Carassius auratus*	27	14	**36.2** **(24.5 - 40.4)**
	Grass Carp *Ctenopharyngodon idella*	1	90	**41.5**
Catfishes	Black Bullhead *Ameiurus melas*	354	120	**26.0** **(11.1 – 66.0)**
	Blue Catfish *Ictalurus furcatus*	4	1	**28.3** **(27.0 - 33.9)**
	Brown Bullhead *A. nebulosus*	183	37	**22.7** **(7.1 – 40.0)**
	Channel Catfish *I. punctatus*	946	147	**43.0** **(15.1 - 78.5)**
Group cont. next page	Flathead Catfish *Pylodictis olivaris*	4	2	**48.0** **(32.4 – 54.0)**

Continued on next page

Table S1 Continued

Species Group	Common Name *Scientific Name*	N	# Waterbodies	Median Fork Length (cm) (min – max)
Catfishes cont.	White Catfish *A. catus*	52	11	**28.0** **(23.9 - 31.5)**
	Yellow Bullhead *A. natalis*	30	6	**21.9** **(17.3 - 29.6)**
	Unspecified bullhead *Ameiurus* spp.	237	18	**23.8** **(14.5 - 55.8)**
	Unspecified catfish	10	4	**56.9** **(35.6 – 67.0)**
Char	Arctic Char *Salvelinus alpinus*	22	3	**26.7** **(18.0 – 58.0)**
	Brook Trout *S. fontinalis*	986	119	**20.9** **(3.9 - 59.3)**
	Bull Trout *S. confluentus*	118	11	**31.9** **(19.3 - 78.8)**
	Dolly Varden *S. malma*	105	14	**18.1** **(1.5 - 60.6)**
	Lake Trout *S. namaycush*	4269	276	**53.0** **(8.6 – 113.4)**
	Splake *S. namaycush* X *S. fontinalis*	61	10	**29.6** **(12.6 - 38.3)**
Chub	Bigeye Chub *Hybopsis amblops*	1	1	**12.8**
	Bonytail Chub *Gila elegans*	2	1	**-**
	Flathead Chub *Platygobio gracilis*	2	1	**-**
	Lake Chub *Couesius plumbeus*	29	3	**11.4** **(8.1 – 14.0)**
	Tui Chub *G. bicolor*	247	22	**8.9** **(3.2 - 35.8)**
	Utah Chub *G. atraria*	28	6	**14.6** **(13.3 - 28.7)**
	Yaqui Chub *G. purpurea*	3	1	**-**
Cichlids	Tilapia *Tilapia* spp.	10	1	21.7 (16.2 – 33.0)
Cisco	Cisco (Lake Herring) *Coregonus artedi*	143	18	**33.5** **(9.0 – 60.5)**
	Least Cisco *C. sardinella*	30	2	**22.3** **(13.5 – 37.0)**
	Unspecified cisco *Coregonus* spp.	67	4	**24.9** **(15.5 – 36.0)**
Clupeiformes	American Gizzard Shad *Dorosoma cepedianum*	18	7	16.9 (3.4 - 36.5)
	American Shad *Alosa sapidissima*	12	2	20.7 (16.8 - 21.2)
	Threadfin Shad *D. petenense*	14	5	16.1 (14.8 - 17.6)
	Unspecified clupiforme	22	1	-

Continued on next page

Table S1 Continued

Species Group	Common Name *Scientific Name*	N	# Waterbodies	Median Fork Length (cm) (min – max)
Crappie	Black Crappie *Pomoxis nigromaculatus*	508	137	**20.7** **(2.7 - 39.2)**
	White Crappie *P. annularis*	105	27	**22.1** **(13.9 - 30.6)**
	Unspecified crappie *Pomoxis* spp.	99	18	**26.3** **(12.2 - 34.5)**
Freshwater Drum	Freshwater Drum *Aplodinotus grunniens*	53	5	**43.5** **(15.0 - 72.3)**
Gar	Longnose Gar *Lepisosteus osseus*	1	1	**74.9**
Goldeye	Goldeye *Hiodon alosoides*	504	10	**33.0** **(13.7 - 42.2)**
Inconnu	Inconnu *Stenodus nelma*	69	5	**65.4** **(44.0 – 93.2)**
Killifish	Desert Pupfish *Cyprinodon macularius*	2	1	**-**
	Pecos Gambusia *Gambusia nobilis*	5	2	-
	Pecos Pupfish *C. pecosensis*	10	2	-
	Plains Killifish *Fundulus zebrinus*	6	2	-
	Sailfin Molly *Poecilia latipinna*	32	1	-
	Western Mosquitofish *G. affinis*	102	22	3.4 (2.4 - 5.2)
Minnows	Brassy Minnow *Hybognathus hankinsoni*	21	4	**4.0** **(3.0 - 9.8)**
	California Roach *Hesperoleucus symmetricus*	13	2	**-**
	Chiselmouth *Acrocheilus alutaceus*	8	5	**21.9** **(15.5 – 30.0)**
	Common Dace *Leuciscus leuciscus*	9	1	**6.1** **(5.1 - 7.1)**
	Emerald Shiner *Notropis atherinoides*	3	2	**7.5** **(7.1 – 8.0)**
	Fathead Minnow *Pimephales promelas*	57	15	**7.4** **(3.8 - 8.2)**
	Finescale Dace *Phoxinus neogaeus*	11	2	**7.9** **(6.0 - 10.8)**
	Golden Shiner *Notemigonus crysoleucas*	14	5	**8.8** **(8.0 - 9.6)**
	Hardhead *Mylopharodon conocephalus*	5	3	**-**
	Hitch *Lavinia exilicauda*	3	2	**23.5**
Group cont. next page	Longnose Dace *Rhinichthys cataractae*	5	1	**-**

Continued on next page

Table S1 Continued

Species Group	Common Name *Scientific Name*	N	# Waterbodies	Median Fork Length (cm) (min – max)
Minnows cont.	Northern Redbelly Dace *Chrosomus eos*	23	3	**7.7** **(6.9 – 9.0)**
	Peamouth *Mylocheilus caurinus*	41	16	**20.9** **(13.7 - 26.4)**
	Pearl Dace *Margariscus margarita*	50	6	**8.1** **(6.5 - 10.9)**
	Red Shiner *Cyprinella lutrensis*	27	8	
	Redside Shiner *Richardsonius balteatus*	17	4	**7.5** **(5.1 - 13.5)**
	Rudd *Scardinius erythropthalmus*	2	2	**33.4** **(30.9 - 35.9)**
	Sacramento Blackfish *Orthodon microlepidotus*	70	5	**34.5** **(18.9 – 46.0)**
	Sand Shiner *Notropis stramineus*	3	2	**4.4** **(3.9 - 9.1)**
	Speckled Dace *Rhinichthys osculus*	10	1	**20.1** **(3.9 - 22.2)**
	Spottail Shiner *Notropis hudsonius*	96	6	**7.0** **(6.5 - 8.3)**
	Unspecified minnow	7	3	**6.6** **(6.5 - 7.1)**
Morone bass	Striped Bass *Morone saxatilis*	417	17	**40.0** **(11.9 - 93.4)**
	White Bass *M. chrysops*	342	33	**30.9** **(10.3 - 60.9)**
	Whiterock Bass *M. chrysops* X *M. saxatilis*	169	20	**36.5** **(10.7 - 71.7)**
Pike	Muskellunge *Esox masquinongy*	19	4	**73.6** **(67.3 - 97.1)**
	Northern Pike *E. Lucius*	13905	860	**59.4** **(8.7 - 130.0)**
	Tiger Muskellunge *E. masquinongy* X *E. lucius*	8	4	**67.5** **(38.7 - 92.4)**
Pikeminnow	Colorado Pikeminnow *Ptychocheilus lucius*	1	1	**-**
	Northern Pikeminnow *P. oregonensis*	141	39	**22.0** **(9.0 - 53.0)**
	Sacramento Pikeminnow *P. grandis*	31	3	**38.5** **(18.5 - 46.7)**
Sculpin	Mottled Sculpin *Cottus bairdii*	1	1	**8.6**
	Prickly Sculpin *C. asper*	10	3	**9.2** **(7.7 - 15.4)**
	Reticulate Sculpin *C. perplexus*	1	1	**-**
Group cont. next page	Riffle Sculpin *C. gulosus*	17	2	**-**

Continued on next page

Table S1 continued

Species Group	Common Name *Scientific Name*	N	# Waterbodies	Median Fork Length (cm) (min – max)
Sculpin cont.	Slimy Sculpin *C. cognatus*	203	12	**5.8** **(4.1 – 12.2)**
	Torrent Sculpin *C. rhotheus*	25	2	**6.4** **(4.4 - 12.6)**
	Unspecified sculpin *Cottus* spp.	9	2	**-**
Stickleback	Brook Stickleback *Culaea inconstans*	3	2	-
	Ninespine Stickleback *Pungitius pungitius*	1	1	4.8
	Threespine Stickleback *Gasterosteus aculeatus*	24	4	4.5 (3.8 - 6.5)
Sturgeon	Lake Sturgeon *Acipenser fulvescens*	44	2	111.5 (42.7 - 155.8)
	Shovelnose Sturgeon *Scaphirhynchus platorynchus*	17	2	-
	White Sturgeon *A. transmontanus*	14	3	130.1 (97.0 - 168.2)
	Unspecified sturgeon	7	2	56.0 (51.0 – 104.0)
Suckers	Bigmouth Buffalo *Ictiobus cyprinellus*	36	5	**57.5** **(35.0 – 73.0)**
	Blue Sucker *Cycleptus elongatus*	3	2	**-**
	Bridgelip Sucker *Catostomus columbianus*	9	4	**33.2** **(29.2 - 42.3)**
	Carpsucker *Carpiodes carpio*	14	7	**42.3** **(31.4 - 50.8)**
	Cui-Ui *Chasmistes cujus*	1	1	**-**
	Flannelmouth Sucker *Catostomus latipinnis*	2	1	**19.7**
	Largescale Sucker *Catostomus macrocheilus*	240	40	**43.0** **(21.8 - 56.3)**
	Longnose Sucker *Catostomus catostomus*	484	42	**37.1** **(6.7 – 61.0)**
	Lost River Sucker *Deltistes luxatus*	3	1	**-**
	Mountain Sucker *Catostomus platyrhynchus*	7	1	**-**
	Quillback *Carpiodes cyprinus*	4	1	**-**
	Razorback Sucker *Xyrauchen texanus*	55	3	**-**
	Sacramento Sucker *Catostomus occidentalis*	62	24	**40.4** **(24.3 - 46.8)**
Group cont. next page	Shorthead Redhorse *Moxostoma macrolepidotum*	11	3	**28.5** **(25.5 – 40.0)**

Continued on next page

Table S1 continued

Species Group	Common Name *Scientific Name*	N	# Waterbodies	Median Fork Length (cm) (min – max)
Suckers cont.	Silver Redhorse *M. anisurum*	14	1	**21.1** **(10.2 - 23.4)**
	Smallmouth Buffalo *I. bubalus*	7	2	**56.2** **(39.6 - 63.9)**
	Tahoe Sucker *Catostomus tahoensis*	6	2	**24.5** **(21.8 - 30.4)**
	Utah Sucker *Catostomus ardens*	18	6	**42.5** **(36.5 - 46.2)**
	White Sucker *Catostomus commersonii*	905	136	**37.5** **(5.3 - 55.4)**
	Unspecified redhorse *Moxostoma* spp.	8	4	**31.8** **(16.0 - 39.4)**
	Unspecified sucker	78	21	**48.0** **(23.8 - 61.8)**
Sunfishes	Bluegill *Lepomis macrochirus*	693	162	**16.3** **(2.6 – 27.0)**
	Bluespotted Sunfish *Enneacanthus gloriosus*	4	1	**16.8** **(14.8 - 19.5)**
	Green Sunfish *L. cyanellus*	94	33	**16.9** **(4.8 – 39.0)**
	Pumpkinseed *L. gibbosus*	63	11	**14.0** **(6.6 - 20.6)**
	Redear Sunfish *L. microlophus*	53	16	**20.7** **(13.1 - 28.8)**
	Rock Bass *Ambloplites rupestris*	11	5	**19.0** **(15.2 - 24.8)**
	Sacramento Perch *Archoplites interruptus*	11	4	**16.3** **(10.8 - 25.7)**
	Tule Perch *Hysterocarpus traskii*	14	3	**12.4**
	Warmouth *L. gulosus*	1	1	**-**
	Unspecified sunfish	4	2	**15.8** **(12.1 - 16.8)**
Trout	Apache Trout *Oncorhynchus apache*	25	3	**32.6** **(25.1 – 37.0)**
	Brown Trout *Salmo trutta*	442	109	**36.7** **(10.5 - 76.6)**
	Chinook Salmon *O. tshawytscha*	128	2	**14.1** **(5.8 – 19.0)**
	Cutthroat Trout *O. clarkia*	773	101	**27.8** **(12.1 - 64.2)**
	Golden Trout *O. aguabonita*	45	1	**15.1** **(11.0 - 17.2)**
	Kokanee *O. nerka*	333	57	**27.9** **(11.5 - 50.5)**
	Lahontan Cutthroat Trout *O. clarkii henshawi*	24	7	**29.3** **(21.3 - 48.5)**
Group cont. next page	Rainbow Trout *O. mykiss*	2364	401	**30.7** **(8.0 - 88.9)**

Continued on next page

Table S1 continued

Species Group	**Common Name** *Scientific Name*	**N**	**# Waterbodies**	**Median Fork Length (cm) (min – max)**
Trout cont.	Redband trout *O. mykiss* sspp.	66	12	**21.5** **(18.2 - 25.1)**
	Tiger trout *S. trutta* X *Salvelinus fontinalis*	30	9	**34.2** **(10.7 - 56.2)**
	Unspecified trout	42	7	**37.4** **(17.2 - 73.4)**
Walleye & Sauger	Sauger *Sander canadensis*	327	23	**39.0** **(18.4 – 55.0)**
	Saugeye *S. canadensis* X *S. vitreus*	24	5	**45.0** **(29.7 - 67.8)**
	Walleye *S. vitreus*	16140	695	**43.2** **(4.5 - 85.7)**
Whitefish	Bonneville Whitefish *Prosopium spilonotus*	20	1	**36.9** **(25.0 - 45.6)**
	Broad Whitefish *Coregonus nasus*	40	6	**43.2** **(36.0 – 53.0)**
	Humpback Whitefish *C. pidschian*	80	4	**43.4** **(30.1 – 59.8)**
	Lake Whitefish *C. clupeaformis*	2893	169	**42.9** **(5.0 – 90.9)**
	Mountain Whitefish *P. williamsoni*	315	31	**24.0** **(8.4 - 44.2)**
	Round Whitefish *P. cylindraceum*	282	22	**33.9** **(17.3 – 55.0)**
	Unspecified whitefish	166	24	**41.9** **(15.3 - 85.5)**
Yellow Perch	Yellow Perch *Perca flavescens*	1958	283	**20.5** **(4.1 - 44.4)**
	Unspecified perch	679	53	**22.0** **(3.4 - 33.2)**

Table S2: Comparison of least squares mean fish total mercury concentrations (µg/g wet weight ± standard error) from lakes and reservoirs using alternative models. Degrees of freedom (D.F.), F-statistic (F), and P-value (P) are given for each comparison.

Ecoregion	# Lakes	# Res	Lake Mean	Reservoir Mean	D.F.	F	P
			Selected Model				
All ecoregions	**1350**	**850**	**0.09 ± 0.006**	**0.13 ± 0.011**	**1, 2146**	**22.59**	**< 0.001**
Great Plains	149	240	0.12 ± 0.010	0.13 ± 0.009	1, 2947	0.24	0.624
Marine West Coast Forest	72	17	0.13 ± 0.013	0.11 ± 0.022	1, 2010	0.28	0.595
Mediterranean California	59	139	0.05 ± 0.007	0.14 ± 0.012	1, 2140	56.51	< 0.001
North American Deserts	84	194	0.09 ± 0.009	0.13 ± 0.010	1, 5198	16.50	< 0.001
Northern Forests	567	6	0.08 ± 0.005	0.12 ± 0.019	1, 19437	8.83	0.003
Northwestern Forested Mountains	280	251	0.11 ± 0.008	0.12 ± 0.009	1, 2239	1.40	0.236
Taiga	139	3	0.10 ± 0.009	0.18 ± 0.067	1, 1723	2.17	0.141
			Selected Model Excluding Rare Taxa				
All ecoregions	**1,323**	**836**	**0.10 ± 0.010**	**0.15 ± 0.016**	**1, 2113**	**23.07**	**< 0.001**
Great Plains	147	239	0.14 ± 0.014	0.15 ± 0.014	1, 2798	1.78	0.182
Marine West Coast Forest	68	16	0.14 ± 0.017	0.13 ± 0.026	1, 1981	0.31	0.578
Mediterranean California	55	138	0.06 ± 0.009	0.16 ± 0.017	1, 2055	52.82	< 0.001
North American Deserts	80	187	0.10 ± 0.012	0.14 ± 0.014	1, 5271	15.88	< 0.001
Northern Forests	563	6	0.09 ± 0.008	0.14 ± 0.023	1, 19305	8.57	0.003
Northwestern Forested Mountains	273	247	0.12 ± 0.012	0.13 ± 0.013	1, 2205	1.29	0.256
Taiga	137	3	0.12 ± 0.012	0.20 ± 0.078	1, 1699	2.21	0.138
			With Soil Mercury ($F_{1,9354}$ = 0.65, P = 0.42)				
All ecoregions	**470**	**750**	**0.09 ± 0.008**	**0.11 ± 0.010**	**1, 1131**	**10.42**	**0.001**
Great Plains	121	174	0.12 ± 0.011	0.12 ± 0.010	1, 1902	0.03	0.858
Marine West Coast Forest	30	14	0.10 ± 0.017	0.09 ± 0.020	1, 988	0.56	0.454
Mediterranean California	48	130	0.05 ± 0.008	0.13 ± 0.013	1, 1065	38.18	< 0.001
North American Deserts	80	489	0.08 ± 0.010	0.13 ± 0.011	1, 3015	9.95	0.002
Northern Forests	-	-	-	-	-	-	-
Northwestern Forested Mountains	191	243	0.11 ± 0.010	0.11 ± 0.010	1, 1169	0.23	0.633
Taiga	-	-	-	-	-	-	-
			With Surface Area ($F_{1,1490}$ = 0.00, P = 0.95)				
All ecoregions	**527**	**783**	**0.10 ± 0.008**	**0.12 ± 0.010**	**1, 1921**	**10.01**	**0.002**
Great Plains	124	195	0.13 ± 0.013	0.12 ± 0.010	1, 2209	0.18	0.675
Marine West Coast Forest	59	17	0.12 ± 0.015	0.11 ± 0.023	1, 1138	0.18	0.669
Mediterranean California	52	136	0.06 ± 0.009	0.13 ± 0.012	1, 1252	28.91	< 0.001
North American Deserts	79	191	0.08 ± 0.010	0.13 ± 0.011	1, 2099	17.06	< 0.001
Northern Forests	-	-	-	-	-	-	-
Northwestern Forested Mountains	213	244	0.11 ± 0.011	0.11 ± 0.010	1, 1504	0.06	0.814
Taiga	-	-	-	-	-	-	-

Table S3: Comparison of species composition (mean % ± standard error) and mean tropic position (± standard error) of fish sampled from lakes and reservoirs throughout the western United States and Canada.

Ecoregion-Foraging Guild	Lakes		Reservoirs	
	Percent of Sample	Trophic Position	Percent of Sample	Trophic Position
Great Plains				
Benthivore	4.4 ± 1.2	2.8 ± < 0.1	7.1 ± 1.1	2.8 ± < 0.1
Planktivore	0.3 ± 0.2	3.4 ± < 0.1	1.7 ± 0.6	3.4 ± < 0.1
Generalist invertivore	2.3 ± 1	3.3 ± < 0.1	2.1 ± 0.6	3.6 ± < 0.1
Generalist	24.9 ± 2.4	3.4 ± < 0.1	20.9 ± 1.8	3.4 ± < 0.1
Piscivore	68.1 ± 2.7	4.2 ± < 0.1	68.1 ± 2.1	4.2 ± < 0.1
Marine West Coast Forest				
Benthivore	3.4 ± 1.9	3 ± < 0.1	0.6 ± 0.4	3 ± < 0.1
Planktivore	2.3 ± 1.3	3.3 ± < 0.1	1 ± 1	3.2 ± < 0.1
Generalist invertivore	8.5 ± 3	3.4 ± < 0.1	19.8 ± 8.2	3.7 ± < 0.1
Generalist	37.4 ± 4.9	3.4 ± < 0.1	23 ± 8.2	3.4 ± < 0.1
Piscivore	48.4 ± 5.1	4.3 ± < 0.1	55.5 ± 10.7	4.2 ± < 0.1
Mediterranean California				
Benthivore	20.6 ± 5.3	3 ± < 0.1	9.2 ± 1.5	3 ± < 0.1
Planktivore	0 ± 0	3 ± 0.1	0 ± 0	3.6 ± < 0.1
Generalist invertivore	11.1 ± 4.8	3.2 ± < 0.1	1.3 ± 0.8	3.2 ± < 0.1
Generalist	8.6 ± 4.4	3.5 ± < 0.1	5.9 ± 1.7	3.5 ± < 0.1
Piscivore	59.8 ± 6.9	4.4 ± < 0.1	83.6 ± 2.4	4.4 ± < 0.1
North American Deserts				
Benthivore	8.8 ± 3.1	3 ± < 0.1	9.6 ± 1.5	3 ± < 0.1
Planktivore	2.7 ± 1.6	3.3 ± < 0.1	1.8 ± 0.6	3.3 ± < 0.1
Generalist invertivore	8.6 ± 3.4	3 ± < 0.1	4.1 ± 1	3.2 ± < 0.1
Generalist	41.1 ± 5.6	3.5 ± < 0.1	36.7 ± 2.9	3.5 ± < 0.1
Piscivore	38.9 ± 5.7	4 ± < 0.1	47.7 ± 2.9	4.1 ± < 0.1
Northern Forests				
Benthivore	1.8 ± 0.4	2.6 ± < 0.1	0.1 ± 0.1	3.2 ± 0.1
Planktivore	2.4 ± 0.4	3.4 ± < 0.1	0.2 ± 0.2	3.4 ± < 0.1
Generalist invertivore	4.9 ± 0.8	3.4 ± < 0.1	2.7 ± 2.7	3.7 ± < 0.1
Generalist	2.8 ± 0.5	3.4 ± < 0.1	5 ± 4.1	3.3 ± < 0.1
Piscivore	88.1 ± 1.2	4.2 ± < 0.1	92 ± 5.1	4.2 ± < 0.1
Northwestern Forested Mountains				
Benthivore	1.7 ± 0.6	3 ± < 0.1	4.7 ± 1	3 ± < 0.1
Planktivore	7.6 ± 1.2	3.4 ± < 0.1	6.6 ± 1.3	3.3 ± < 0.1
Generalist invertivore	27.6 ± 2.4	3.5 ± < 0.1	5.9 ± 1.3	3.5 ± < 0.1
Generalist	42.9 ± 2.6	3.4 ± < 0.1	47.9 ± 2.8	3.5 ± < 0.1
Piscivore	20.2 ± 2.1	4 ± < 0.1	34.8 ± 2.7	4.1 ± < 0.1
Taiga				
Benthivore	1.9 ± 0.7	2.8 ± < 0.1	-	-
Planktivore	28.4 ± 2.7	3.4 ± < 0.1	61.3 ± 18.2	3.4 ± < 0.1
Generalist invertivore	0.9 ± 0.6	3.4 ± < 0.1	-	-
Generalist	0.3 ± 0.3	3.4 ± < 0.1	-	-
Piscivore	68.6 ± 2.7	4.1 ± < 0.1	38.7 ± 18.2	3.9 ± < 0.1

Table S4: Distribution of reservoirs, sample size, and sampling years among reservoir ages.

Reservoir Age	# Res	N	Sampling Years	Reservoir Age	# Res	N	Sampling Years
0	3	254	1991 - 1993	**41**	40	574	1972 - 2011
1	4	224	1984 - 1994	**42**	36	550	1973 - 2009
2	10	211	1970 - 2007	**43**	38	466	1970 - 2008
3	9	275	1970 - 1997	**44**	26	543	1971 - 2010
4	10	336	1971 - 1997	**45**	38	802	1971 - 2011
5	9	118	1972 - 2007	**46**	27	547	1984 - 2012
6	9	174	1970 - 1999	**47**	30	166	1970 - 2011
7	10	87	1969 - 2001	**48**	23	249	1982 - 2012
8	13	126	1970 - 2011	**49**	22	193	1980 - 2011
9	7	93	1971 - 2002	**50**	20	209	1973 - 2011
10	10	133	1972 - 2010	**51**	31	504	1986 - 2011
11	9	230	1969 - 2011	**52**	32	386	1982 - 2011
12	13	332	1970 - 2009	**53**	28	325	1984 - 2011
13	13	143	1971 - 2010	**54**	31	257	1970 - 2012
14	18	145	1971 - 2007	**55**	28	242	1982 - 2011
15	7	25	1970 - 1997	**56**	15	111	1985 - 2010
16	11	176	1970 - 2009	**57**	17	223	1971 - 2014
17	9	24	1970 - 2006	**58**	16	127	1970 - 2011
18	17	116	1970 - 2011	**59**	16	114	1970 - 2011
19	14	86	1973 - 2008	**60**	14	119	1981 - 2011
20	11	45	1984 - 2008	**61**	15	109	1972 - 2010
21	19	209	1972 - 2004	**62**	15	221	1974 - 2011
22	18	266	1970 - 2001	**63**	16	302	1970 - 2007
23	11	266	1980 - 2011	**64**	16	54	1972 - 2007
24	19	130	1970 - 2005	**65**	17	127	1970 - 2011
25	27	142	1977 - 2011	**66**	13	64	1971 - 2012
26	15	88	1980 - 2006	**67**	16	83	1982 - 2008
27	19	162	1970 - 2011	**68**	20	183	1989 - 2009
28	29	338	1970 - 2010	**69**	26	341	1979 - 2011
29	19	275	1971 - 2007	**70**	21	426	1985 - 2011
30	20	150	1970 - 2007	**71**	16	118	1985 - 2011
31	35	288	1970 - 2011	**72**	27	240	1984 - 2010
32	23	423	1970 - 2011	**73**	9	95	1994 - 2012
33	23	224	1970 - 2010	**74**	15	161	1992 - 2012
34	23	227	1972 - 2007	**75**	12	86	1995 - 2012
35	25	258	1972 - 2011	**76**	18	154	1986 - 2011
36	22	490	1977 - 2011	**77**	13	67	1991 - 2012
37	29	354	1979 - 2010	**78**	12	106	1989 - 2012
38	36	541	1977 - 2008	**79**	13	106	1986 - 2009
39	26	261	1970 - 2011	**80**	18	156	1985 - 2010
40	47	558	1971 - 2011	**81**	13	116	1986 - 2011

Continued on next page

Table S3 Continued

Reservoir Age	# Res	N	Sampling Years	Reservoir Age	# Res	N	Sampling Years
82	8	85	1992 - 2011	**131**	2	42	2001 - 2011
83	11	86	1991 - 2011	**132**	2	7	2008
84	11	115	1994 - 2011	**133**	2	16	2005 - 2008
85	7	58	1991 - 2008	**136**	1	19	2008
86	12	107	1992 - 2011	**137**	2	14	2007
87	8	28	1991 - 2010	**139**	1	20	2011
88	6	31	1992 - 2007	**141**	1	6	2007
89	11	82	2000 - 2011	**148**	1	19	2003
90	9	138	2001 - 2011	**151**	1	11	2007
91	8	18	1998 - 2008	**157**	1	4	2007
92	13	152	1999 - 2012				
93	9	65	1997 - 2007				
94	6	58	2005 - 2012				
95	9	52	2002 - 2010				
96	14	96	2003 - 2011				
97	9	108	1989 - 2012				
98	5	29	2005 - 2008				
99	10	91	1992 - 2011				
100	9	92	2006 - 2011				
101	4	29	2006 - 2008				
102	3	9	1990 - 2007				
103	3	31	2007 - 2011				
104	4	39	2006 - 2009				
105	1	3	2007				
106	8	161	2005 - 2011				
107	1	3	2008				
108	1	8	2001				
109	1	10	2006				
110	1	3	1991				
111	1	20	2011				
113	3	9	2005 - 2008				
114	1	6	2008				
115	4	32	2007 - 2008				
116	2	15	2007				
117	1	8	2007				
118	3	4	1994 - 2010				
119	2	24	2007				
123	1	3	2008				
124	1	4	2006				
129	1	25	2011				

Literature Cited

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