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Reduced trace element concentrations in fast-growing juvenile Atlantic salmon in natural streams

Darren M. Ward^{1,*}, Keith H. Nislow², Celia Y. Chen¹, and Carol L. Folt¹

¹Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA

²Northern Research Station, USDA-USFS, University of Massachusetts, Amherst, MA, 01003, USA

Abstract

To assess the effect of rapid individual growth on trace element concentrations in fish, we measured concentrations of seven trace elements (As, Cd, Cs, Hg, Pb, Se, Zn) in stream-dwelling Atlantic salmon (*Salmo salar*) from 15 sites encompassing a 10-fold range in salmon growth. All salmon were hatched under uniform conditions, released into streams, and sampled ~120 days later for trace element analysis. For most elements, element concentrations in salmon tracked those in their prey. Fast-growing salmon had lower concentrations of all elements than slow-growers, after accounting for prey concentrations. This pattern held for essential and non-essential elements, as well as elements that accumulate from food and those that can accumulate from water. At the sites with the fastest salmon growth, trace element concentrations in salmon were 37% (Cs) to 86% (Pb) lower than at sites where growth was suppressed. Given that concentrations were generally below levels harmful to salmon and that the pattern was consistent across all elements, we suggest that dilution of elements in larger biomass led to lower concentrations in fast-growing fish. Streams that foster rapid, efficient fish growth may produce fish with lower concentrations of elements potentially toxic for human and wildlife consumers.

Keywords

bioaccumulation; growth dilution; mercury; stream food web; trace metal; trophic transfer

Introduction

Accumulation of potentially toxic trace elements in fish is a serious ongoing concern for human and wildlife health. In addition to direct toxic effects of elevated trace element concentrations on fish in heavily contaminated areas (1), fish from thousands of inland streams, rivers, and lakes have been declared as unsafe for unrestricted human consumption because of concerns about exposure to toxic trace elements and other contaminants (2). Wildlife species that consume contaminated fish are also at risk. Studies have linked elevated concentrations of Hg and other toxic trace elements in blood or tissue of fish, birds and mammals with negative effects such as reduced reproductive success, hormonal changes, and motor skill impairment (3,4).

Elevated trace elements concentrations in fish are often associated with industrial pollution, residual contamination from past mining activity (1), or other human land use (5,6). However,

^{*}darren.ward@dartmouth.edu; Phone: 603-646-0396; FAX: 603-646-1347.

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even where inputs of trace elements are similar, concentrations in fish and other aquatic organisms vary tremendously due to variation in biological and environmental factors that drive trace element uptake and accumulation (7,8). The overall goals of our work are to identify the most important ecological factors responsible for increasing trace element accumulation in fish under natural conditions in the field. This will improve our capacity to model and predict trace element concentrations *in situ*, and to identify sites and environmental conditions which are most likely to produce fish with elevated concentrations of elements of concern for human and wildlife health.

Variation in individual growth rate of fish should, in principle, dramatically affect trace element concentrations. All else equal, increased growth will reduce whole-body trace element concentrations in fast-growing fish relative to slow growers by somatic growth dilution (SGD). SGD occurs when fast growers assimilate more biomass relative to the specific trace element than slow growers; hence, the element becomes diluted by the extra body mass (9,10). However, translating this principle to the field is complicated and at present there is little consensus on the overall influence of rapid growth on trace element concentration. For example, for trace elements accumulated from food, increased growth due solely to increased intake of prey and associated trace elements will not lead to SGD (11). Despite clear experimental evidence for strong SGD of trace elements in some systems (10,12), empirical studies disagree on the magnitude (13) and even direction (14–16) of the relationship between fish growth rate and trace element accumulation is critical, because individual growth is one of the most variable biological parameters across fish populations, and growth is highly sensitive to fisheries management activities and anthropogenic impacts (17).

We used a unique field assay to measure concentrations of essential and non-essential potentially toxic trace elements (As, Cd, Cs, Hg, Pb, Se, and Zn) in free-living juvenile Atlantic salmon (*Salmo salar*) across a gradient in individual growth. We stocked newly-hatched Atlantic salmon from controlled initial conditions across multiple streams and collected samples after one growing season to measure trace element concentrations in salmon and their prey. Because we used stocked fish, we could ensure that exposure time, initial mean size, and initial mean element concentration were uniform across all sites. Therefore, our samples provide a standardized measure of trace element accumulation and growth across the study sites. We selected relatively pristine study sites that were not impacted by point-source contamination and that produced a wide range in salmon growth rate, associated with variation in the amount of prey available (17). We took this approach in order to isolate the effects of growth rate without confounding from high variation in trace element inputs or direct toxic effects of elevated trace element concentrations on fish physiology.

Methods

We sampled 15 study sites located on 5 small (< 7 m average summer width) tributary streams of the Connecticut River in New Hampshire and Massachusetts (3 sites per stream; site descriptions in (17,18). All of the streams were in predominantly forested watersheds, with no known mining activity or point sources of trace element contamination. We used juvenile Atlantic salmon, stocked as part of an ongoing population restoration program in the study basin (19), as a field assay of trace element accumulation. The salmon were produced at the White River National Fish Hatchery in Bethel, VT and stocked on 13–16 May 2005. All stocked salmon were unfed fry that were still utilizing yolk resources. We released 200, 600, or 1800 fry at each site for companion studies we conducted on density-dependent survival and growth of salmon (17,18). There is no natural Atlantic salmon moving among sites during the growing season (18). Therefore, we could ensure that the underyearling salmon we sampled

at each site were from our controlled stocking events. We collected four underyearling salmon from each site for trace element analysis from 7–9 September 2005 (116–117 days after stocking). We collected fish with a backpack electrofisher, conducting a single pass through a 50–150 m reach immediately downstream of the release site. Salmon were immediately euthanized and transported on ice to a freezer for storage until processing.

We removed stomach contents of all fish prior to processing for trace elements. Undigested stomach contents from the foregut of all fish within a site were composited and processed separately from fish to estimate trace element concentration in salmon prey. Previous studies show that undigested stomach contents can provide a useful index of trace element concentrations in fish prey (20,21). While stomach samples from a single time point could potentially miss important seasonal variation, diets of underyearling salmon in our study area are overwhelmingly dominated by a few taxa of aquatic invertebrates (predominantly Ephemeroptera, Baetidae and Diptera, Chironomidae) throughout the summer growing season (21–23). These taxa accounted for >60% of the volume of salmon stomach contents at all of our sites. In subsequent years we have found nearly identical relationships between fish and prey Hg concentrations when prey were collected separately from fish throughout the growing season (D.M. Ward unpublished data). Thus, we treat the composited gut contents as a reliable index of site-specific trace element concentrations in prey.

Fish and prey samples were freeze dried and the whole sample (for samples < 1 g dry weight) or a homogenized subsample (for samples > 1 g dry weight) were digested in Optima grade nitric acid in sealed Teflon vessels in a microwave reaction accelerator (Mars5, CEM USA, Matthews, NC). Trace element concentrations in the digested solution were measured by inductively coupled plasma mass spectrometry (Agilent 7500cx, Agilent, Santa Clara, CA). Quality control was ensured by analysis of certified reference materials, duplicate samples, and digestion blanks with every processing batch of 20 samples.

We measured several additional biotic and abiotic characteristics of all study sites. At each site we measured mean stream water pH through the growing season (Oakton pH Testr 2, Oakton Instruments, Vernon Hills, IL; biweekly measurements in the field), base flow alkalinity (inflection point titration with sulfuric acid in 2007), mean water temperature (Onset Optic StowAway, Onset Computer Corporation, Pocasset, MA; hourly measurements by loggers anchored to the stream bed), the biomass of benthic invertebrate prey (6 Surber samples, 500 μ m mesh, combined biomass of aquatic Ephemeroptera and Diptera), overhead canopy cover (tubular densitometer, mean of 6 measures per site), and the percent of wetland and forested area in the catchment (24).

Data analysis

The response variables for our primary analyses were trace element concentrations in individual salmon. We had two primary predictors of interest, individual growth (measured as final dry mass) and the concentration of the specific element in prey (measured from composited stomach contents at the site level). Some of the trace elements we measured (e.g. As, Cd, Pb, Zn) can accumulate in fish from water as well as from food. We did not measure aqueous metal concentrations. However, controlled laboratory exposures of juvenile salmonids to known food and water concentrations show that uptake from prey accounts for much of the variation in trace element concentrations of juvenile salmonids even across a wide range of water concentrations (1,25–27). Therefore, using prey concentrations to partially account for variation in trace element exposure across sites is a valid approach in this analysis.

To estimate the effect of suppressed growth on trace element concentrations in fish across individuals and sites while accounting for variation in prey concentrations, we used multi-level linear models with an additive random classification term indicating each site, mean salmon

mass and prey concentration as covariates at the site level, and individual deviations from sitemean mass as a covariate at the individual level. To account for differences in stream water chemistry, we also tested whether adding stream-water pH or alkalinity as predictors at the site level improved model fit. For all covariates at the site level, we used the number of sites as the denominator degrees of freedom. In all analyses, trace element concentrations and fish mass were log₁₀-transformed to yield approximately normal residual variance and linear relationships. In supplementary material (Table S1), we also present pair-wise correlations among all trace elements and correlations of element concentrations with measured site characteristics to aid in identification of habitat factors associated with increased trace element accumulation in stream food webs. Data analysis was conducted using JMP 5.0 and the R program for statistical computing (28,29).

Results

The study sites encompassed a wide range in salmon growth and trace element concentration. Mean individual growth (as final dry mass) varied more than 10-fold across sites (one-way analysis of variance (ANOVA): $F_{14,45}$ =37.0, P<0.0001, r^2 =0.92), with low growth rates associated with low prey biomass (17). All element concentrations varied significantly across sites (one-way ANOVAs; all $F_{14,45}>4.5$, P<0.0001, $r^2>0.58$). Mean concentrations of Cd, Cs, Hg, and Pb all ranged more than 10-fold across sites (maximum/minimum site mean Cd: 14.9; Cs: 13.6; Hg: 10.3; Pb: 59.0), while mean concentrations of As and the essential elements Se and Zn varied less across sites (maximum/minimum site mean As: 2.8; Se: 6.6; Zn: 3.7). All element concentrations in prey and fish were well below levels associated with toxic effects in fish, except for the highest Se concentrations (ref. ³⁰;Table S2). Se is an essential element with a very narrow range between deficient and toxic concentrations (31), so even though concentrations were not particularly high compared to Se contaminated areas, two of our sites and eight individual fish had Se concentrations associated with reduced fish health in sensitive species (2 ppm in prev, 4 ppm in fish; ref. 30). However, excluding the sites and individuals with elevated Se did not affect results. The element concentrations we observed in salmon exceeded no effects hazard concentrations for piscivorous wildlife (4) for Hg (10 sites), Se (2 sites), and Zn (1 site; Table S3).

Mean Cd, Cs, Hg, and Se concentrations in salmon tracked those in their prey across sites, while As concentrations in salmon were marginally related to As in prey and Pb and Zn concentrations were unrelated in salmon and prey (Figure 1, Table 1). Only Hg biomagnified, resulting in element concentrations in salmon t hat were consistently higher than those in their prey; As, Cd, and Cs consistently biodiminished, resulting in element concentrations in salmon that were consistently lower than those in their prey (Figure 1). Fast-growing salmon had lower trace element concentrations for a given concentration in prey (Figure 2). In the regression model including prey concentrations, all trace element concentrations in salmon were significantly lower at sites with high mean individual salmon mass (Table 1). Across individuals, all element concentrations were lower in relatively large individuals within sites, although this relationship within sites was only marginally significant for Hg and Cs (Table 1). Adding pH or alkalinity to the model did not significantly increase the variance explained for any trace element (all P>0.21).

Discussion

Fast growth was associated with lower trace element concentrations in fish for a given concentration in prey, consistent with SGD. This pattern held for essential (Se, Zn), non-essential (As, Cd, Cs, Hg, Pb), and potentially toxic elements (both essential and non-essential at elevated concentrations), as well as elements that accumulate largely from food (Cs, Hg, Se) and those that can accumulate from water (As, Cd, Pb, Zn). Based on the regression slopes,

rapid growth potentially reduced mean element concentrations between 1.6 (Cs) and 7 (Pb) fold across the 10-fold range in growth at our study sites. This result is critically important for management and prediction of levels of trace elements and persistent contaminants in fish, as a common starting point for assessment of fish contamination risk is to assume constant accumulation from water or prey to fish regardless of fish growth rate (32). Further, our results support the general hypothesis that high biological productivity and rapid fish growth can reduce concentrations of toxic trace elements in aquatic food webs (11,33–35).

We suggest that fast growth reduced whole-body concentrations of trace elements in salmon regardless of whether they accumulate from food or water. For elements that accumulate from food, this means that fast growth is likely associated with high growth efficiency – a larger gain in biomass for each gram of food, and food-born trace elements, consumed (9,10). An increasing number of studies indicate that variation in growth efficiency, mediated by differences in prey quality or variation i n energetic costs, is a key driver of variation in growth rate for fish and other aquatic organisms (10,36,37). If variation in growth efficiency frequently drives variation in fish growth rate, SGD should be a common mechanism reducing element concentrations in fish, consistent with our observations.

For elements that accumulate from water, increased biomass should reduce element concentrations in fast growers via SGD as long as rapid growth is not associated elevated exposure. At an individual level, increased respiration rate can increase exposure to aqueous metals via the gills (38), but rapid respiration is not consistently associated with rapid growth of fish (37). Across our study sites, salmon growth was potentially spatially confounded with aqueous exposure because sites with low prey biomass and low fish growth also had relatively low pH and alkalinity (Table S1) – water quality factors associated with increased aqueous metal bioavailability and accumulation (39). However, adding pH or alkalinity as predictors did not explain significant additional variation concentration of any of the trace elements in our analysis. Further, the comparison across individual salmon within sites was not affected by this potential spatial confounding yet relatively fast-growing individuals also had lower trace elements is not conclusive without aqueous concentration data, we suggest that SGD drove the similar relationships for elements that accumulate from either food or water.

We assessed the potential for SGD for whole-body trace element concentrations in salmon, but trace element concentrations vary across tissues within individual fish. For example, elements accumulated from water are often elevated in the gills, while those accumulated from food are elevated in the intestine (25). Whole-body SGD may not be associated with reduced trace element concentrations within individual organs, yet the toxic effects of trace elements on fish often depend on organ-specific concentrations (1,25–27). Therefore, it is unlikely that SGD will reduce toxic effects of trace elements on individual fish. Nonetheless, whole-body SGD can dramatically reduce potential trophic transfer of toxic trace elements to piscivorous fish and wildlife that consume whole fish (11).

Rapid growth was associated with lower element concentrations for all elements we analyzed, yet there were different patterns of accumulation in fish associated with the physiological role of specific elements. In particular, variation across sites in the concentrations of the essential elements Se and Zn was much lower than for all other elements except As. Arsenic is not generally recognized as essential, yet feeding trials indicate that As may have a beneficial or essential function at ultra trace concentrations in wide variety of taxa (31). Thus, lower variation in the concentration of As, Se, and Zn relative to Cd, Cs, Hg, and Pb is potentially due to tighter physiological regulation of essential or potentially beneficial trace elements (40). However, concentrations of all elements, including essential elements, varied substantially across sites, indicating that even the essential trace elements are not under strict homeostatic control.

The correlation between element concentration and body size is one of the most frequently reported metrics for trace elements in fish (41), yet the drivers of this scaling relationship are not known for most elements. Unlike our controlled assay, fish age and size are confounded in most field studies, so these relationships can not be used to assess SGD. Yet, controlled laboratory exposures have shown that allometric scaling relationships can generate concentration-body size relationships for trace elements in fish independent of age or SGD. For example, metal-accumulating tissues in the intestine, kidney, or gills may be a smaller proportion of total body mass in larger fish, yielding negative relationships between wholebody concentrations and body size. This is not the case for intenstine (42), kidney (43), and gills (44) in growing juvenile Atlantic salmon, suggesting that this was not mechanism driving the whole-body SGD that we observed. For many elements, assimilation efficiency from food increases with body size, while elimination rate and specific growth rate decline with body size - scaling relationships that should drive positive relationships between element concentrations and body size (45–47). These allometric scaling relationships may partly account for the elevated trace element concentrations in larger, older fish typical for some elements (9), but can not explain the SGD pattern we observed. In contrast, negative allometric scaling of mass-specific consumption rate and mass-specific uptake rate of water-born trace elements could drive negative concentration-body size relationships consistent with those we observed (45,47). Thus, these mechanisms may have contributed to the SGD pattern of reduced trace element concentrations in large, fast-growing fish that we observed.

Rapid growth can reduce concentrations of trace elements and other contaminants in fish, relative to prey or water exposure sources (11,48,49). Yet, the resultant concentrations in the fish clearly depend critically on the concentrations in the source of exposure. Our results confirm earlier studies showing that, comparing across sites, many trace elements in fish track the concentrations in their prey (50,51). Given the key role of prey concentrations, managing for increased individual growth rate and SGD alone can not mitigate trace element contamination in fisheries (16). However, whereas contaminant inputs and concentrations in prey may not be amenable to short-term, local292 scale control, individual growth is one of the most variable characteristics of fish populations (52) and fish growth is sensitive to anthropogenic manipulations (16,17,49). In fact, increasing individual growth of fish is a frequent target for fisheries management, yet the potential for this widespread fisheries management goal to reduce trace element concentrations in fish remains largely unknown.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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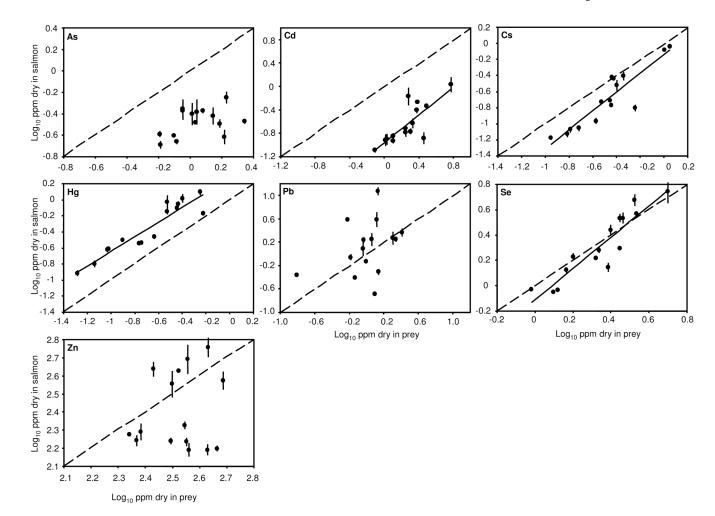


Figure 1.

Scatterplots of trace element concentrations in salmon and their prey across sites. Each point is one site; error bars are ± 1 SE for salmon concentrations. The solid lines are linear fits of salmon concentration to prey concentration and are only shown where this relationship is statistically significant (P<0.05). The dashed line is the 1:1 line, so points above this line indicate element concentration in fish exceed those in prey (biomagnifying), while points below indicate element concentration in fish are less than those in prey (biodimishing).

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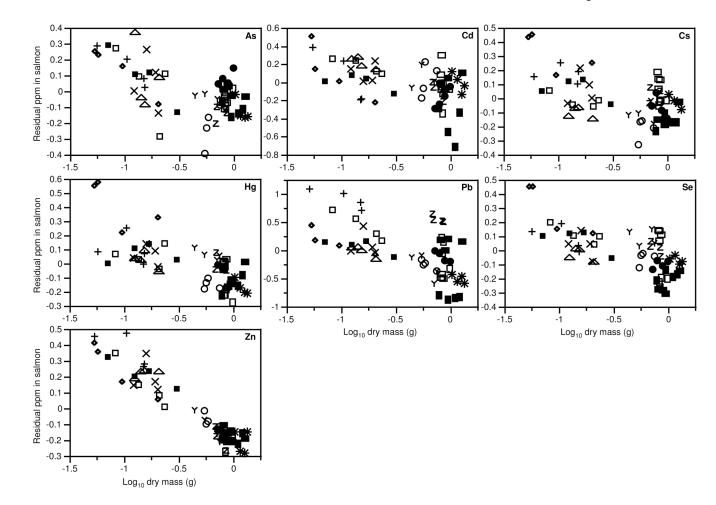


Figure 2.

Scatterplots of residual trace element concentrations, after accounting for variation in concentrations in prey, and salmon dry mass. Dry mass is an index of growth rate as fish started at uniform initial mean size across sites and all fish were similar age at sampling. Each point is one individual salmon, different symbols indicate the different sites.

Table 1

Regression results for all element concentrations in fish s amples. The "log₁₀ prey ppm" predictor is the element concentration in prey for the same element deviation of each individual fish from the site mean dry mass. Slopes are the coefficient estimates for each predictor from the hierarchical linear model, SE as the response in each model. The "Mean log₁₀ dry mass" predictor is the mean dry mass (g) of fish at the site, while "Individual log₁₀ dry mass" is the is the standard error of the slope, P is the P-value.

	\log_1	log ₁₀ prey ppm	mq	Mean]	Mean log ₁₀ dry mass	y mass	Individu	Individual log ₁₀ dry mass	lry mass
Response	Slope	SE	Р	Slope	SE	Р	Slope	SE	Р
log ₁₀ As ppm	0.33	0.13	0.02	-0.21	0.05	<0.01	-0.50	0.11	<0.01
log ₁₀ Cd ppm	0.71	0.17	<0.01	-0.44	0.09	<0.01	-0.53	0.15	<0.01
log ₁₀ Cs ppm	1.23	0.12	<0.01	-0.20	0.08	0.03	-0.13	0.08	0.10
log ₁₀ Hg ppm	0.59	0.07	<0.01	-0.40	0.05	<0.01	-0.16	0.08	0.05
\log_{10} Pb ppm	-0.68	0.63	0.30	-0.86	0.26	0.01	-0.72	0.13	<0.01
log ₁₀ Se ppm	0.63	0.16	<0.01	-0.42	0.06	<0.01	-0.31	0.07	<0.01
log ₁₀ Zn ppm	0.03	0.08	0.67	-0.49	0.02	<0.01	-0.45	0.06	< 0.01