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Rapid, efficient growth reduces mercury concentrations in stream-dwelling Atlantic salmon

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Abstract

Mercury (Hg) is a potent toxin that biomagnifies in aquatic food webs. Large fish generally have higher Hg concentrations than small fish of the same species. However, models predict that fish that grow large faster should have lower Hg concentrations than small, slow-growing fish due to somatic growth dilution (SGD). We examined the relationship between Hg concentrations and growth rate in fish using a large-scale field experiment. Atlantic salmon (*Salmo salar*) fry hatched under uniform initial conditions were released at eighteen sites in natural streams, collected after one growing season, and Hg concentration and growth measured. As expected for Hg accumulation from food, mercury concentrations in salmon tracked Hg concentrations in their prey. Nonetheless, large, fast-growing salmon had lower Hg concentrations than small, slow-growing salmon, consistent with SGD. While prey Hg concentration accounted for 59% of the explained variation in salmon Hg concentration across sites, salmon growth rate accounted for 38% of the explained variation independent of prey Hg concentration. A mass-balance Hg accumulation model shows that such SGD occurs when fast growth is associated with high growth efficiency. Fish growth is tremendously variable and sensitive to anthropogenic impacts, so SGD of Hg has important implications for fisheries management.

INTRODUCTION

Mercury (Hg) contamination in fish is a serious health risk because fish consumption is the primary mode of exposure to toxic methylmercury (MeHg) for humans and wildlife (Mergler et al. 2007; Scheuhammer et al. 2007). Mercury enters the environment from both natural sources and widespread atmospheric deposition from anthropogenic Hg pollution (e.g. coal burning, incinerators) and makes its way into all water bodies (Fitzgerald et al. 1998; Wiener et al. 2006). Deposition from nearby industrial sources can lead to elevated Hg concentrations in fish at a regional scale, including sites in our New England study area (Evers et al. 2007). However, even in areas of elevated deposition, Hg concentrations in fish vary tremendously (Wiener et al. 2006; Driscoll et al. 2007), driven both by environmental factors that increase Hg bioavailability and by ecological processes that increase Hg uptake and accumulation in the food web (Pickhardt et al. 2002; Chen et al. 2005; Evers et al. 2007). Identifying the characteristics of aquatic ecosystems that lead to increased Hg concentration in fish is essential for identifying populations at risk, avoiding management practices that could exacerbate Hg

accumulation, and developing strategies to alleviate Hg contamination in fisheries (Mailman et al. 2006; Munthe et al. 2007).

Studies in freshwater lakes have identified many factors that can promote Hg accumulation, yet Hg accumulation in stream fish has received relatively little attention. Most studies of heavy metal contamination in stream food webs address sites impacted by point sources (Quinn et al. 2003). However, recent studies show that Hg concentrations in stream fish can reach levels dangerous to human and wildlife consumers even in streams with no point sources of Hg (Castro et al. 2007; Peterson et al. 2007). Understanding Hg dynamics in stream food webs is essential because stream fisheries are often intensively harvested (Post et al. 2002; Allan et al. 2005), including millions of hatchery-propagated juvenile fish released in North American streams each year for eventual harvest (Trout Unlimited 1998; Caudill 2005). Furthermore, streams are important sites for the movement of Hg between habitats: streams integrate Hg inputs from the watershed (Scherbatskoy et al. 1998), are a source of Hg to terrestrial consumers of aquatic fauna (Cristol et al. 2008), and act as conduits of Hg to downstream aquatic systems (Schuster et al. 2008).

Fish accumulate MeHg, the highly toxic form of Hg that biomagnifies in food webs, almost entirely from consumption of contaminated prey (Hall *et al.* 1997). Relative to inorganic Hg, MeHg is efficiently assimilated from food and is highly persistent in organisms, so nearly all of the Hg in higher trophic-level consumers is MeHg (Bloom 1992). Given this trophic accumulation, high MeHg concentrations in prey are an important indicator of sites at increased risk of high MeHg concentrations in fish. If the proportion of total Hg as MeHg in prey is consistent, relatively inexpensive measurements of total Hg concentrations in prey can also predict fish concentrations, as seen in many studies in lakes (e.g. Chen et al. 2000, 2005). There is little direct evidence linking spatial variation in prey total Hg or MeHg concentration to variation in fish Hg concentration in stream ecosystems, and contradictory patterns have been found (Castro et al. 2007). Thus, further investigations linking variation in Hg concentration in stream fish and their prey are needed to determine the risks associated with increased Hg concentrations at the base of stream food webs.

Fish size and growth rate also exert powerful effects on Hg accumulation. One nearly ubiquitous finding in field investigations of Hg accumulation in fish is that larger individuals have higher Hg concentrations than small individuals of the same species (Trudel and Rasmussen 2006). However, simple mass-balance models of Hg accumulation predict that, all else equal, individuals that grow to large size quickly will have lower Hg concentration than smaller, slow-growing individuals due to somatic growth dilution (SGD) (Karimi et al. 2007). Higher Hg concentration in larger fish is likely due to large fish feeding on more-contaminated prey at higher trophic levels (Trudel and Rasmussen 2006). Predictions of SGD do not contradict this relationship; SGD suggests that, for a given age and prey intake, fish that grow to a larger size will have lower Hg concentration because they accumulate more biomass relative to Hg than slow growers. Some studies suggest that SGD may be a key factor driving variation in fish Hg concentration (Rennie et al. 2005; Simoneau et al. 2005). Furthermore, manipulating fish growth shows some promise as a means to manage Hg contamination in fisheries (Verta 1990; Essington and Houser 2003; Surette et al. 2003). However, given the confounding effects of changes in fish diet composition with size and the lack of data about fish age in most field studies, SGD has proven extremely difficult to detect in field studies and empirical evidence for strong SGD of Hg in the field remains equivocal (Stafford and Haines 2001; Trudel and Rasmussen 2006; Lepak et al. 2009).

To evaluate the importance of prey Hg concentration and individual growth for determining Hg concentration in stream fish, we examined the relationships between Hg concentration in fish, Hg concentration in prey, and individual growth and size using a large-scale field

experiment in natural streams. We released newly-hatched Atlantic salmon (*Salmo salar* L.) from uniform initial conditions at eighteen sites and collected them after one growing season to measure Hg concentration. This is the first study to use controlled releases of fish in natural streams to measure variation in Hg accumulation.

METHODS

Field study

The 18 study sites were located on 6 small (< 7 m average summer width) tributary streams in the Connecticut River basin in New Hampshire and Massachusetts (3 sites per stream; site descriptions in Ward et al. 2008). There were no known point sources of Hg on any of the study streams. Atmospheric Hg deposition monitoring stations near the northernmost and southernmost sites showed similar concentrations of Hg in rainfall at the extremes of the 200-km north to south spatial range of the sites (Miller et al. 2005; National Atmospheric Deposition Program 2007), although dry Hg deposition was likely higher for the southern sites (Evers et al. 2007).

We stocked juvenile Atlantic salmon, produced at the White River National Fish Hatchery in Bethel, VT, in the study streams in both 2005 and 2006 (13–16 May 2005 and 8–9 May 2006). All salmon were reared in the same conditions in the hatchery and were stocked as fry before they transitioned from yolk resources to feeding. We collected a subsample of fry at the time of stocking to measure initial size (2005: mean = 0.18 g; SD = 0.03; 2006: mean = 0.15 g; SD = 0.03) and Hg concentration (2005: <1 ng/g wet; 2006: mean = 1.0 ng/g wet; SD = 0.12). Three stocking density treatments (low: 200 fry; medium: 600 fry; high: 1800 fry) were randomly assigned to the sites within each stream for companion studies on density-dependent survival and growth (Ward et al. 2008, 2009).

There is no natural reproduction by Atlantic salmon in the study streams and the salmon we stocked were the only salmon introduced at the study sites in 2005 and 2006. Furthermore, the sites were separated sufficiently (most > 1 km apart, four were ca. 800 m) that mixing of juvenile salmon among sites within the summer was unlikely (Einum and Nislow 2005) and we observed clear gaps in the distribution of salmon between adjacent sites in spatially extensive fish sampling (Ward et al. 2008). Therefore, we assumed that the underyearling salmon we sampled in this study were all from our controlled stocking events and came from the nearest release site.

We collected underyearling salmon from each site for Hg analysis from 7–9 September 2005 (116–117 d after stocking) and 19–28 September 2006 (133–143 d 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 and capturing a minimum of four underyearling salmon per site. Salmon for Hg analysis were euthanized (cranial concussion and pithing) and transported on ice to a freezer for storage until processing. Over both years, there were five sites (3 in 2005, 2 in 2006) where we did not collect any underyearling salmon for Hg analysis due to poor survival of the stocked fish (Ward et al. 2008). These sites are missing in all analyses, leaving 15 sites (66 individual fish) for analyses for 2005 and 16 sites (89 fish) for 2006.

We removed stomach contents of all fish prior to processing for Hg. Undigested stomach contents from the foregut of all fish within a site were composited and processed separately from the fish to estimate Hg concentration in invertebrate prey. Fish and prey samples were freeze dried and the whole sample (sample < 1 g dry weight) or a homogenized subsample (sample > 1 g dry weight) digested in 5 mL ultra-pure HNO₃ and 2 mL nanopure water in Teflon vessels in a microwave reaction accelerator (CEM Mars5, CEM Corporation, Matthews, NC).

Total mercury concentration in the digested solution was measured by inductively coupled plasma mass spectrometry. The detection limit for Hg at the average sample mass was <0.1 ng/g wet weight. Each processing batch of 20 fish samples included certified standards (mussel tissue NIST-SRM 2976 or dogfish muscle NRCC-DORM-2) and procedural blanks. Standard measurements averaged 99% (SD = 9%) of the certified concentration. All blanks were <1% of the average concentration in samples. Average recovery from ten samples spiked with known Hg concentrations was 100.9%. The average relative percent difference of ten samples analyzed in duplicate was 5.2%. We used the measured relationship between wet mass and dry mass to convert dry basis measurements to wet basis to facilitate comparison with other studies.

We did not measure the proportion of Hg as MeHg in samples, so all Hg concentrations we report are total Hg measurements. However, in salmon sampled in 2008 from many of the same sites as this study, we found that nearly all of the Hg in underyearling salmon was MeHg (mean = 96%; SD = 3%; N=27; D.M.W. unpublished data), consistent with other observations for MeHg in fish tissue (Bloom 1992). The proportion of Hg as MeHg in prey invertebrates is generally lower and more variable than in predatory fish (Mason et al. 2000). However, the strong relationship of prey Hg concentration and fish Hg concentration across sites and the consistent biomagnification between fish and prey (see Results) suggest that the proportion of Hg as MeHg in prey was consistent across sites. In samples of mayflies (Baetidae and Heptageniidae) from 2008, we found that the proportion of Hg as MeHg averaged 85% (SD = 10%; N=20; D.M.W. unpublished data).

Previous studies have shown that undigested stomach contents are representative of metal concentrations in fish prey (Kennedy et al. 2004; Tucker and Rasmussen 1999). While our stomach samples from a single time point could potentially miss important seasonal variation in diet composition and prey Hg concentration, spring and summer diets of underyearling Atlantic salmon in this system are overwhelmingly dominated by a few taxa of aquatic invertebrates throughout the growing season (predominantly Ephemeroptera, Baetidae and Diptera, Chironomidae; see Kennedy et al. 2004, 2008; Grader and Letcher 2006). These taxa accounted for >60% of the volume of stomach contents at all of our sites. Furthermore, in subsequent years of sampling we found nearly identical relationships between prey Hg and salmon Hg when the primary prey (baetid mayflies) were collected separately from fish through the growing season (D.M.W. unpublished data). Thus, we treat the composited gut contents as reliable indicators of site-specific prey Hg concentrations.

We measured several biotic and abiotic characteristics of the study sites, including those identified in other studies as important predictors of Hg concentration in fish. At each site we measured the biomass of benthic invertebrate prey (six Surber samples, 500 µm mesh, combined biomass of aquatic Ephemeroptera and Diptera), stream water pH (Oakton pH Testr 2, Oakton Instruments, Vernon Hills, IL), overhead canopy cover (tubular densitometer, mean of six measures per site), stream temperature (mean of hourly measurements from loggers anchored to the stream bed) and the percent of wetland and forested area in the catchment (land cover data from Moore et al. 2004). In previous studies, reduced biomass of invertebrate prey was associated with increased Hg concentration in fish and their prey in lakes (Chen and Folt 2005), low pH was associated with increased Hg concentration in fish and prey in both lakes and streams (Chen et al. 2005; Mason et al. 2000), and increased shading from overhead canopy was associated with suppressed algal growth and increased Hg concentration in benthic stream algae (Hill and Larsen 2005). Wetlands are important methylation sites for Hg and increased wetland area in the catchment is associated with increased Hg concentration in fish in lakes and streams (Castro et al. 2007; Driscoll et al. 2007).

Data analysis

The primary response we assessed was final Hg concentration of individual salmon. We had two primary predictors of interest, individual salmon growth (measured as final mass) and Hg concentration in the prey (measured from composited stomach contents at the site level). Final mass is a reliable estimate of growth rate in this study due to the similar initial size at release and age at capture of fish across sites. In all analyses, Hg concentration and fish mass were $\log_{10}$ transformed to equalize variance and linearize relationships. Salmon growth was bimodally distributed; very low growth in two study streams in both years yielded a clumped relationship between growth and Hg concentration (Figure 1). However, analyzing the high-growth and low-growth sites separately did not change the overall conclusions for SGD, so we analyzed all sites together. We first used a multi-level linear model (Qian and Shen 2007) to test the effect of the predictors on salmon Hg concentration, analyzing the years separately. The model contained an additive random classification term indicating each site, with mean salmon mass and prey Hg concentration as covariates at the site level, and individual deviations from site-mean mass as a covariate at the individual level. We used the number of sites as the denominator degrees of freedom for the covariates at the site level (15 in 2005, 16 in 2006). To test the effect of our stocking density treatments on mean salmon Hg at each site, we used a general linear mixed model with stream and year as additive random factors, stocking density as a fixed factor, and prey Hg as a covariate. In a separate analysis, we used hierarchical partitioning of site-mean salmon Hg concentration to estimate the independent contribution of prey Hg concentration, mean mass, and year to explained variation in salmon Hg concentration (Mac Nally 2002). In the hierarchical partitioning analysis, we combined both years due to the similarity of patterns across years. We used correlation analyses to test for pairwise relationships between the biotic and abiotic stream characteristics and mean Hg concentration in salmon and prey. All statistical analysis was conducted using the R program for statistical computing (R Development Core Team 2008)

Mass-balance model

To determine whether the observed low Hg concentrations in fast-growing fish were consistent with SGD, we applied a simple, widely-used contaminant mass balance model (Luoma and Rainbow 2005; Trudel and Rasmussen 2006; Karimi et al. 2007;). The model, assuming uptake from water is negligible (Hall et al. 1997), is defined by $Hg_{ss} = (AE \cdot SIR \cdot C_f \cdot P) \cdot (K_e + G)^{-1}$, where Hg_{ss} is fish Hg concentration at steady state (ng/g; assumed to be all methylmercury), AE is assimilation efficiency, SIR is specific ingestion rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$), C_f is the total Hg concentration in the food (ng/g), P is the proportion of Hg as MeHg in the prey (0.85, see below), K_e is Hg efflux (d^{-1}), and G is specific growth ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$). We modified the model by incorporating the P term in order to use literature values for MeHg accumulation in fish with our total Hg measurements in prey. This steady-state model is useful for evaluating the range of conditions that lead to increased or decreased Hg concentration in fish (Trudel and Rasmussen 2006). Furthermore, simulations with a standard dynamic model (Hanson et al. 1997) parameterized for juvenile salmon indicate that juvenile salmon rapidly approach Hg_{ss} , given the C_f , temperature, and growth rates we observed (<50 days). To facilitate comparison of the model results with our field data, we converted G to mass after 100 days using an initial size of 0.2 g.

We parameterized the model by setting G and C_f over the ranges observed from field data and manipulating SIR across the range reported in the literature for juvenile Atlantic salmon (0.02 to $0.08 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$; Kennedy et al. 2004, 2008; Tucker and Rasmussen 1999); the upper bound of this range is consistent with functional models for maximum ingestion rate of a 1-g Atlantic salmon (Nislow et al. 2000; Forseth et al. 2001). Comparing the literature estimates of SIR to the growth rates we observed in the field yields estimated growth efficiencies ($G \cdot SIR^{-1}$) covering the range of empirical estimates for stream-dwelling juvenile Atlantic salmon (10%

to 60%; Tucker and Rasmussen 1999; Kennedy et al. 2008) and other stream salmonids (Morinville and Rasmussen 2003) and consistent with growth efficiency estimates from the functional model (Forseth et al. 2001). We estimated K_e as 0.008, using the equation of Trudel and Rasmussen (1997) which predicts K_e from fish size and temperature. Our estimate is the mean of daily estimates over the growing season, given daily mean temperature measurements (averaged across streams) and assuming constant growth rate. The AE was set at 0.8, following Trudel and Rasmussen (2006). We estimated P as 0.85 based on our samples taken at these sites in 2008 (observed range 0.7–1.0). In comparing our results to our empirical data, we assume that P does not vary across sites, but setting P as constant does not affect our interpretation of the model with regard to the potential for SGD.

RESULTS

Field study

After 116–143 days in natural streams, salmon Hg concentration ranged from 21 to 342 ng/g (wet mass basis) across all individuals (all results are for total Hg concentrations). In both years, individual salmon within sites had similar Hg concentrations and most of the variance in salmon Hg concentration was across sites (r^2 of one-way ANOVA of individual salmon Hg concentration across sites 2005: $r^2 = 0.95$; 2006: $r^2 = 0.85$). The spatial pattern of mean salmon Hg concentrations across sites was similar over the two study years (correlation of site mean Hg concentration across years $r = 0.74$; $N=13$; $P=0.004$).

Salmon Hg concentration was significantly related to prey Hg concentration and salmon growth, with consistent patterns across both years (Figure 1). Mercury concentrations in salmon tracked Hg concentrations in their prey across sites (Figure 1; 2005: slope = 0.58; SE = 0.08; $F_{1,15} = 41.6$; $P < 0.0001$; 2006: slope = 0.65; SE = 0.16; $F_{1,16} = 16.6$; $P = 0.0009$), while increased mean growth (as final size) yielded decreased mean Hg concentration across sites (Figure 1; 2005: slope = -0.62; SE = 0.10; $F_{1,15} = 41.7$; $P < 0.0001$; 2006: slope = -0.27; SE = 0.12; $F_{1,16} = 5.2$; $P = 0.04$). Furthermore, relatively large individual salmon had lower Hg concentrations within sites in 2005 (slope = -0.32; SE = 0.15; $F_{1,48} = 4.6$; $P = 0.04$), with a similar but not statistically significant trend within sites in 2006 (slope = -0.11; SE = 0.10; $F_{1,70} = 0.7$; $P = 0.4$). Stocking density treatments did not significantly affect mean salmon Hg concentrations ($F_{2,21} = 0.2$, $P = 0.8$).

Hierarchical partitioning of explained variation in site-mean salmon Hg concentration showed that growth accounted for 38% of explained variation independent of prey Hg concentration. Prey Hg concentration accounted for 59% of explained variation and 3% of explained variation was due to differences across years. The full model (including growth, prey Hg, and year) explained 83% of the total variation in mean salmon Hg concentration across sites.

Salmon and prey Hg concentrations were consistently correlated with biotic and abiotic characteristics of the study sites. Sites with low pH, low prey biomass, high canopy cover, and heavily forested catchments generally had higher Hg concentrations in both salmon and prey (Table 1). In contrast, mean stream temperature and wetland area in the catchment were not significantly correlated with Hg concentrations in biota (Table 1).

Mass-balance model

As observed in the field study, the model predicts that C_f (Hg concentration in food) is a key driver of Hg_{ss} (steady-state Hg concentration in salmon; Figure 2a). For any constant growth efficiency, an increase in C_f yields a directly proportional increase in Hg_{ss} . Also consistent with the field study, the model indicates that variation in G (growth) can generate considerable variation in Hg_{ss} independent of C_f (Figure 2b). In order to produce a negative relationship

between Hg_{ss} and G , as we observed in the field, increased G must be associated with increased growth efficiency. Increased G due solely to increased SIR (specific ingestion rate) yields increased Hg_{ss} , the opposite of SGD (somatic growth dilution, Figure 2b). The effect of increasing growth efficiency on Hg_{ss} depends on both K_e (efflux rate) and SIR . For K_e of 0.008, as we estimated for underyearling salmon, increasing growth efficiency from 10% to 60% yields a 2.0 ($SIR=0.02$) to 3.5-fold ($SIR=0.08$) decline in Hg_{ss} across all values of C_f . The overall modeled SGD relationship between G and Hg_{ss} , when bounded by the range of literature estimates of SIR and growth efficiency, closely matches our empirical observations (compare Figure 1 and Figure 2).

DISCUSSION

This study represents one of the clearest empirical examples of SGD as a determinant of fish Hg concentration in the field. As expected for Hg accumulation through the food web, prey Hg concentration was the most important predictor of salmon Hg concentration, accounting for 59% of explained variation. However, mean individual growth rate accounted for 38% of the explained variation in mean salmon Hg concentration independent of prey Hg concentration. Consistent with SGD, larger, fast-growing fish had lower Hg concentrations; our regression estimates suggest that fast growth reduced mean mercury concentrations 37–57% across the range of growth rates we observed across sites in 2005 and 2006. This inverse relationship between Hg concentration and size directly contrasts the pattern of high Hg concentration in large fish reported in many field studies, underscoring the importance of accounting for growth rate (i.e., age) and not just size when assessing Hg accumulation dynamics in fish. We likely observed this growth effect so clearly because juvenile Atlantic salmon of these sizes in streams do not switch to a markedly higher trophic-level diet as they grow larger (Grader and Letcher 2006), so increasing Hg concentrations in prey did not confound the effects of increased growth rate (Trudel and Rasmussen 2006). However, even for fish that do feed on more-contaminated prey at higher trophic levels as they grow, yielding higher Hg concentrations in larger fish, SGD can reduce Hg concentrations for fish of a given size or age (Simoneau et al. 2005). Our mass-balance model analysis showed that strong SGD of Hg occurs when variation in growth efficiency drives variation in growth rates. We conclude that suppressed fish growth rate, associated with low growth efficiency, increases the susceptibility of aquatic ecosystems to Hg contamination in fish.

We used a conservation stocking program for Atlantic salmon as a model system for this study (Folt et al. 1998). The salmon we sampled were from a protected population and were too small for harvest by humans, although the Hg concentrations in salmon that we observed are a potential concern for predators of juvenile salmon (Figure 1). However, our finding that stocked, juvenile fish rapidly accumulate Hg and reflect site-specific drivers of Hg accumulation is directly relevant to Hg monitoring programs. State and federal agencies stock millions of fish in US lakes and streams each year (Trout Unlimited 1998; Caudill 2005), many as juveniles that require substantial growth and have the potential for substantial mercury accumulation before reaching harvestable size. With coordination of stocking efforts across targeted sites, measuring Hg concentration in these stocked fish allows for a sampling design with the species, age, exposure time, and initial Hg concentrations of fish all standardized across sites. Other systems where small, juvenile fish are stocked and grow to harvestable size in areas with no natural reproduction are also ideal for this approach (put-grow-and-take fisheries), including many North American fisheries for walleye (*Stizostedion vitreum*) (Li et al. 1996) and esocids (Wahl 1995). Using stocked fish that are intended for harvest as an assay of Hg accumulation is particularly relevant for quantifying human Hg exposure and for developing consumption advisories that protect human health (Lepak et al. 2009).

While prey Hg concentrations clearly drive Hg accumulation in fish, Hg levels in prey may not be amenable to control short-term, local-scale control. Thus, clarifying the importance of SGD in determining fish Hg concentration is particularly important because individual growth of fish is highly variable (e.g., more than 10-fold variation across sites in this study) and sensitive to anthropogenic impacts and fisheries management, with important implications for Hg accumulation (Verta 1990; Essington and Houser 2003; Surette et al. 2003). In many fisheries, high stocking density leads to suppressed fish growth rate due to density-dependent growth, potentially exacerbating Hg accumulation. We observed that high stocking density led to suppressed mean individual growth of salmon, but the effect of stocking density on growth was very small relative to total variation in growth driven by variation in prey biomass (Ward et al. 2009) and increased stocking density did not lead to significantly increased Hg concentrations in salmon. However, other studies have shown that intensive fishing in order to reduce fish population density can lead to increased growth rates and reduced Hg concentrations in fish (Verta 1990; Surette et al. 2003). In addition to fish stocking and removal, harvest regulations such as size limits are often specifically implemented in order to maximize fish growth rates, potentially reducing Hg accumulation, yet the implications for Hg concentrations in harvested fish remain unknown.

Our modeling approach shows that strong SGD occurs when variation in growth efficiency drives variation in fish growth rates (see also Rennie et al. 2005; Trudel and Rasmussen 2006), yet the general importance of variation in growth efficiency for driving variation in fish growth in the field is not clear. Many bioenergetics models attribute variation in fish growth to variation in prey consumption by default (Hanson et al. 1997), leading some studies to conclude that the potential effects of SGD on Hg concentration in fish are minimal (Stafford and Haines 2001). However, recent studies show that variation in growth efficiency, mediated by variation in activity costs, can be a key driver of growth variation in fish (Trudel and Rasmussen 2001), even overriding the effects of variation in consumption (Rennie et al. 2005). For salmon, we found that individuals grew faster (Ward et al. 2009) and had lower Hg concentrations at sites with high prey biomass, implying higher growth efficiency at these sites. This effect may be mediated by changes in foraging behavior yielding higher growth efficiency at high prey availability. Orpwood et al. (2006) found that juvenile Atlantic salmon reduced the energy expended in active foraging at high prey availability, suggesting an increase in growth efficiency.

Both prey Hg concentration and individual growth directly affect fish Hg concentration, yet these direct controls are themselves controlled by biotic and abiotic characteristics of the local environment. We found increased prey Hg concentrations, and consequently increased salmon Hg concentrations, at sites with low pH, low prey biomass, high canopy cover, and heavily forested catchments. In contrast to other studies in both streams and lakes (Castro et al. 2007; Driscoll et al. 2007), we did not find higher Hg concentration in biota at sites with more wetland area in the catchment. Wetlands are potentially important sites for conversion of inorganic Hg to MeHg and sources of MeHg to downstream ecosystems, particularly during runoff episodes. However, recent studies indicate that there is potential for substantial production of MeHg in stream sediments during the growing season (Schuster et al. 2008), which may be a more important continuous source of MeHg to stream-dwelling organisms in these systems than periodic flux from upstream wetlands.

Our findings extend some key patterns identified in studies of Hg accumulation in freshwater lakes to stream systems for the first time. In particular, Hg concentration in lake fish and their invertebrate prey is often highest at apparently pristine, oligotrophic lakes with low primary productivity and prey biomass (Chen et al. 2000; Pickhardt et al. 2002; Chen and Folt 2005). While this matches the pattern we observed across streams, with higher Hg concentration at heavily-shaded sites with low prey biomass and low fish growth rates, it remains unclear

whether similar mechanisms drive these relationships in lake and stream food webs. Dilution of Hg by increased algal biomass (bloom dilution) and prey biomass, along with individual SGD in primary consumers, leads to reduced Hg concentration in biota from more-productive lakes (Pickhardt et al. 2002; Karimi et al. 2007). Hill and Larsen (2005) showed that similar bloom dilution of Hg occurs at the base of stream food webs when increased light stimulates increased algal production. However, in our study streams, heavily-shaded sites with low prey biomass and high prey Hg concentration also had low pH. Low pH can increase Hg bioavailability and methylation rates (Gilmour and Henry 1991), potentially leading to increased Hg concentration in prey and confounding the apparent effects of bloom dilution and increased prey biomass across our study streams. In addition, fish grew slower at sites with low prey biomass (Ward et al. 2009), so reduced SGD also contributed to increased Hg concentration in fish at these sites. Thus, while this study clearly demonstrates the important direct role of prey Hg concentration and growth in determining Hg concentrations in stream fish, future research should determine how correlated biotic and abiotic environmental factors drive variation in prey Hg concentration, fish growth and growth efficiency to affect Hg accumulation in fish.

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Figure 1.

Relations between (a) site-mean salmon mercury concentration ($\pm$ SE) and prey mercury concentration in 2005 (filled points) and 2006 (open points), (b) mercury concentration and individual mass for all salmon analyzed in 2005 and 2006. Individual mass reflects growth due to uniform age and initial size. The arrows indicate MeHg critical values for fish-eating mammals (100 ng/g) and birds (20 ng/g) (Yearley et al. 1998).

Figure 2.

(a) Model predicted steady-state mercury concentrations ($H_{g,ss}$) in salmon for the range in prey Hg concentration (C_p) observed in the empirical study, with growth efficiency (GE) ranging from 10% to 60% and ingestion rate (SIR) held constant at $0.08 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$. (b) Model-predicted $H_{g,ss}$ for a range of growth rates (G , expressed as size at 100 days) with variation in growth generated either by varying SIR with growth efficiency held constant (dashed lines labeled with corresponding SIR) or by varying growth efficiency with consumption rate held constant (solid lines labeled with corresponding GE); prey Hg concentration held constant at 100 ng/g.

Summary of site characteristics and their correlations with Hg concentrations in prey invertebrates and juvenile Atlantic salmon over both study years. Correlation coefficients (*r*) are followed by *P*-values; correlations with *P*<0.05 are in bold text.

Table 1

Site characteristic	Mean (SD)	Range	Prey Hg <i>r</i> (<i>P</i> -value)		Salmon Hg <i>r</i> (<i>P</i> -value)	
			2005	2006	2005	2006
Canopy cover (%; site)	65 (23)	30–93	0.56 (0.03)	0.30 (0.26)	0.79 (<0.01)	0.58 (0.02)
Forest area (%; catchment)	80 (11)	54–97	0.45 (0.09)	0.52 (0.04)	0.37 (0.18)	0.72 (<0.01)
Mean temperature (°C)	14.7 (1.0)	12.4–16.8	–0.01(0.99)	0.25(0.34)	0.14(0.62)	–0.03(0.92)
pH	6.8 (0.4)	6.3–7.4	–0.84 (<0.01)	–0.49 (0.06)	–0.96 (<0.01)	–0.78 (<0.01)
Prey biomass (mg/m ²)	8.2 (6.4)	1–21	–0.51 (0.05)	–0.35 (0.18)	–0.73 (<0.01)	–0.52 (0.04)
Wetland area (%; catchment)	3 (1)	1–5	–0.14 (0.61)	0.15 (0.59)	0.03 (0.91)	0.02 (0.95)