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[Article]

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 will have lower Hg concentrations than small, slow-growing fish owing to somatic growth dilution (SGD). We examined the relationship between Hg concentration and growth rate in fish by means of a large-scale field experiment. Atlantic salmon *Salmo salar* fry hatched under uniform initial conditions were released at 18 sites in natural streams, collected after one growing season, and measured with respect to Hg concentration and growth. As expected for Hg accumulation from food, the Hg concentrations in the fish tracked those in their prey. Nonetheless, large, fast-growing fish had lower Hg concentrations than small, slow-growing ones, consistent with SGD. While the Hg concentration of the prey accounted for 59% of the explained variation in the Hg concentration in the Atlantic salmon across sites, the salmon growth rate accounted for 38%. 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 the SGD of Hg has important implications for fisheries management.

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 via both natural sources and atmospheric deposition resulting from anthropogenic pollution (e.g., coal-burning plants and 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, the Hg concentrations in fish vary tremendously (Wiener et al. 2006; Driscoll et al. 2007), being driven both by environmental factors that increase the bioavailability of Hg and ecological processes that increase its 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 concentrations in fish is essential for identifying the populations at risk, avoiding management practices that could exacerbate the accumulation of Hg, 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 such 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 the Hg dynamics in stream food webs is essential because stream fish are often intensively harvested (Post et al. 2002; Allan et al. 2005), including the millions of hatchery-propagated juvenile fish released into 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.

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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 the 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 ratio of MeHg to total Hg in prey is consistent, relatively inexpensive measurements of total Hg concentrations in prey can be used to predict those of MeHg in fish, as has been shown in many studies in lakes (e.g., Chen et al. 2000, 2005). However, there is little direct evidence linking the spatial variation of the total Hg or MeHg concentration in prey to the variation in fish in stream ecosystems, and contradictory patterns have been found (Castro et al. 2007). Thus, further investigations of the variations in Hg concentration in stream fish and their prey are needed to determine the risks associated with higher 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 large individuals have higher 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 concentrations than smaller, slow-growing individuals owing to somatic growth dilution (SGD; Karimi et al. 2007). The higher Hg concentrations observed in large fish are probably due to 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 a lower Hg concentration because they accumulate more biomass relative to Hg than do slow growers. Some studies suggest that SGD is a key factor behind the variation in Hg concentrations in fish (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 such studies and empirical evidence for the strong SGD of Hg in the field remains equivocal (Stafford and Haines 2001; Trudel and Rasmussen 2006; Lepak et al. 2009a).

To evaluate the importance of prey Hg concentration and individual growth to the concentration of Hg in stream fish, we examined the relationships between the Hg concentration of fish, that of their prey, and individual growth and size using a large-scale field experiment in natural streams. We released newly hatched Atlantic salmon *Salmo salar* from uniform initial conditions at 18 sites and collected them after one growing season to measure their Hg concentration. This is the first study to use controlled releases of fish in natural streams to measure the 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 are given 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; NADP 2007), although dry Hg deposition was probably higher at the southern sites due to proximity to industrial sources (Evers et al. 2007).

We stocked juvenile Atlantic salmon produced at the White River National Fish Hatchery in Bethel, Vermont, in the study streams in both 2005 and 2006 (13–16 May 2005 and 8–9 May 2006). All of these fish were reared under the same conditions in the hatchery and stocked as fry before they transitioned from yolk resources to feeding. We collected a subsample of fry at the time of stocking to measure their initial sizes (2005: mean = 0.18 g; SD = 0.03; 2006: mean = 0.15 g; SD = 0.03) and Hg concentrations (2005: mean < 1 ng/g wet; 2006: mean = 1.0 ng/g wet; SD = 0.12). Three stocking density treatments (low = 200 fry, medium = 600 fry, and high = 1,800 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 ones that we stocked were the only Atlantic salmon introduced at the study sites in 2005 and 2006. Furthermore, the sites were sufficiently separated (most were more than 1 km apart, though four were ~800 m apart) that mixing among sites within the summer was unlikely (Einum and Nislow 2005) and we observed clear gaps in the distribution of fish between adjacent sites in spatially extensive

sampling (Ward et al. 2008). Therefore, we assumed that the underyearling Atlantic salmon that we sampled in this study were all from our controlled stocking events and came from the nearest release site.

We collected underyearling Atlantic salmon for Hg analysis from each site from 7 to 9 September 2005 (116–117 d after stocking) and from 19 to 28 September 2006 (133–143 d after stocking). We collected these 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. Those for Hg analysis were euthanatized (cranial concussion and pithing) and transported on ice to a freezer for storage until processing. Over both years, there were five sites (three in 2005, two in 2006) at which we did not collect any underyearling salmon owing to the poor survival of the stocked fish (Ward et al. 2008). These sites were excluded from all of our analyses, leaving 15 sites (66 individual fish) for analysis for 2005 and 16 sites (89 fish) for 2006.

We removed the stomach contents of all fish before processing them for Hg analysis. The undigested stomach contents from the foreguts of all fish at a site were composited and processed separately from the fish to estimate the Hg concentration of invertebrate prey. Fish and prey samples were freeze-dried and the whole sample (samples <1 g dry weight) or a homogenized subsample (samples >1 g) digested in 5 mL of ultrapure HNO_3 and 2 mL of nanopure water in Teflon vessels in a microwave reaction accelerator (CEM Mars5; CEM Corporation, Matthews, North Carolina). The total Hg concentration in the digested solution was measured by inductively coupled plasma mass spectrometry. The detection limit for Hg at the average sample mass was less than 0.1 ng/g of 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 less than 1% of the average concentration in the samples. The average recovery from 10 samples spiked with known Hg concentrations was 100.9%. The average relative percent difference of 10 samples analyzed in duplicate was 5.2%. We used the measured relationship between wet mass and dry mass to convert measurements on a dry basis to ones on a wet basis to facilitate comparison with other studies.

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

Previous studies have shown that undigested stomach contents accurately reflect the metal concentrations in fish prey (Tucker and Rasmussen 1999; Kennedy et al. 2004). While our stomach samples from a single time point could miss important seasonal variation in diet composition and Hg concentration, the spring and summer diets of the underyearling Atlantic salmon in this system are dominated by a few taxa of aquatic invertebrates throughout the growing season (predominantly Ephemeroptera, Baetidae and Diptera, and Chironomidae; see Kennedy et al. 2004, 2008; Grader and Letcher 2006). These taxa accounted for more than 60% of the volume of stomach contents at all of our sites. Furthermore, in sampling in subsequent years we found nearly identical relationships between the Hg concentrations of prey and Atlantic salmon when the primary prey (baetid mayflies) were collected separately from the fish over the growing season (D.M.W., unpublished data). Thus, we treated 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 concentrations 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, Illinois), 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 percentage of wetland and forested area in the catchment (land cover data from Moore et al. 2004). In previous studies, lower biomasses of invertebrate prey were associated with higher Hg concentrations in fish and their prey in lakes (Chen and Folt 2005), lower pH values were associated with higher Hg concentrations in fish and their prey in both lakes and streams (Mason et al. 2000; Chen et al. 2005), and more overhead canopy was associated with

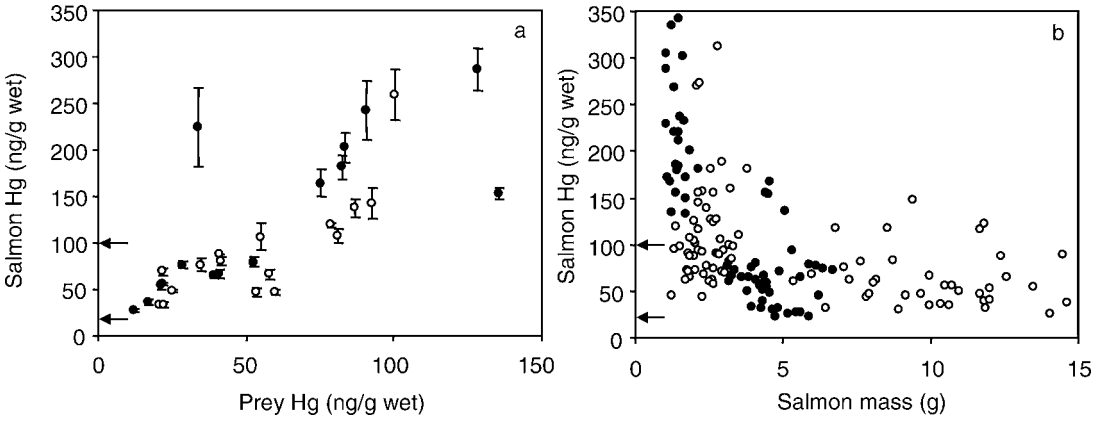

FIGURE 1.—Relationships between **(a)** the site-mean Hg concentration in Atlantic salmon and that in their prey in 2005 (filled circles) and 2006 (open circles) and **(b)** Hg concentration and individual mass for all fish analyzed; the error bars denote SEs. Because of the uniform age and initial size of the fish, individual mass reflects growth. The arrows indicate the critical values for MeHg for fish-eating mammals (100 ng/g) and birds (20 ng/g) (Yeardley et al. 1998).

less algal growth and higher Hg concentrations in benthic stream algae (Hill and Larsen 2005). Wetlands are important methylation sites for Hg, and more wetland area in the catchment is associated with higher Hg concentrations in fish in lakes and streams (Castro et al. 2007; Driscoll et al. 2007).

Data analysis.—The primary response that we assessed was the final Hg concentration of individual Atlantic salmon. There were two primary predictors of interest: the growth of individual salmon (measured as final mass) and the Hg concentration in the prey (measured from the composited stomach contents at the site). Final mass was a reliable estimate of growth rates in this study owing to the similar initial sizes at release and ages at capture of fish across sites. In all analyses, Hg concentration and fish mass were $\log_{10}$ transformed to equalize the variance and linearize the 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 about SGD, so we analyzed all sites together. We first used a multilevel linear model (Qian and Shen 2007) to test the effects of the predictors on salmon Hg concentration, analyzing the years separately. The model contained an additive random classification term indicating the site as well as mean salmon mass and prey Hg concentration as covariates at the site level and individual deviations from the mean mass at the site 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 the mean salmon Hg concentration 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 concentration as a covariate. In a separate analysis, we used hierarchical partitioning of site mean salmon Hg concentrations to estimate the independent contributions of prey Hg concentration, mean mass, and year to the explained variation in the salmon Hg concentration (Mac Nally 2002). In this analysis, we combined both years owing to the similarity of the patterns across years. We used correlation analyses to test for pairwise relationships between the biotic and abiotic stream characteristics and the mean Hg concentrations in the salmon and their prey. All statistical analyses were conducted with 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 that Hg uptake from water is negligible (Hall et al. 1997), is defined by the equation

$$\mathrm{Hg_{ss}} = (\mathrm{AE}\cdot \mathrm{SIR}\cdot C_f \cdot P)/(K_e + G),$$

where $\mathrm{Hg_{ss}}$ is the fish Hg concentration at steady state (ng/g; assumed to be all methylmercury), AE is the assimilation efficiency, SIR is the specific ingestion rate ($\mathrm{g}\cdot\mathrm{g}^{-1}\cdot\mathrm{d}^{-1}$), C_f is the total Hg concentration in the food (ng/g), P is the proportion of MeHg in the prey (0.85; see below), K_e is the Hg efflux (per day), and G is the specific growth rate ($\mathrm{g}\cdot\mathrm{g}^{-1}\cdot\mathrm{d}^{-1}$). We modified

the usual model by incorporating P so that we could use literature values for MeHg accumulation in fish with our total Hg measurements for prey. This steady-state model is useful for evaluating the range of conditions that lead to increased or decreased Hg concentrations in fish (Trudel and Rasmussen 2006). Furthermore, simulations with a standard dynamic model (Hanson et al. 1997) parameterized for juvenile Atlantic salmon indicate that they rapidly approach Hg_{ss} (<50 d) given the C_f, temperature, and growth rates that we observed. To facilitate comparison of the model results with our field data, we converted G to mass after 100 d using an initial size of 0.2 g.

We parameterized the model by setting G and C_f to values in the ranges from field data and manipulating SIR across the range reported in the literature for juvenile Atlantic salmon (0.02–0.08 $g \cdot g^{-1} \cdot d^{-1}$; Tucker and Rasmussen 1999; Kennedy et al. 2004, 2008); the upper bound of this range is consistent with functional models for the maximum ingestion rate of a 1-g Atlantic salmon (Nislow et al. 2000; Forseth et al. 2001). Comparing the literature estimates of SIR with the growth rates that we observed in the field yields estimated growth efficiencies (G/SIR) that cover the range of empirical estimates for stream-dwelling juvenile Atlantic salmon (10–60%; Tucker and Rasmussen 1999; Kennedy et al. 2008) and other stream salmonids (Morinville and Rasmussen 2003) and that are consistent with the 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 the daily estimates over the growing season, given the daily mean temperature measurements (averaged across streams) and assuming a constant growth rate. The value of AE was set at 0.8 following Trudel and Rasmussen (2006). We estimated P as 0.85 based on samples taken at these sites in 2008 (observed range, 0.7–1.0). In comparing our results with our empirical data, we assumed that P does not vary across sites, but this does not affect our interpretation of the model with regard to the potential for SGD.

Results

Field Study

After 116–143 d in natural streams, our fish had total Hg concentrations ranging from 21 to 342 ng/g (wet mass basis). In both years, the fish within sites had similar Hg concentrations and most of the variance was across sites (one-way analysis of variance; 2005: $r^2 = 0.95$; 2006: $r^2 = 0.85$). The spatial pattern of the mean Hg concentrations across sites was similar over the two study years ($r = 0.74$, $N = 13$, $P = 0.004$).

The Hg concentration in the fish was significantly related to that in the prey and to fish growth, with consistent patterns across years (Figure 1). The Hg concentrations in the fish tracked those in their prey across sites (2005: slope = 0.58, SE = 0.08, $F_{1, 15} = 41.6$, $P < 0.0001$; 2006: slope = 0.65, SE = 0.16, $F_{1, 16} = 16.6$, $P = 0.0009$; Figure 1), while greater mean growth (as determined from the final size) yielded lower mean Hg concentrations across sites (2005: slope = −0.62, SE = 0.10, $F_{1, 15} = 41.7$, $P < 0.0001$; 2006: slope = −0.27, SE = 0.12, $F_{1, 16} = 5.2$, $P = 0.04$; Figure 1). 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 Hg concentrations ($F_{2, 21} = 0.2$, $P = 0.8$).

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

Fish and prey Hg concentrations were consistently correlated with the 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 fish and prey (Table 1). In contrast, mean stream temperature and wetland area in the catchment were not significantly correlated with Hg concentrations (Table 1).

Mass-Balance Model

As observed in the field study, the model predicts that C_f (the Hg concentration in prey) is a key driver of Hg_{ss} (the steady-state Hg concentration in fish; 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). To produce a negative relationship between Hg_{ss} and G, as we observed in the field, a higher value for G must be associated with increased growth efficiency. A higher G that is due solely to a higher SIR (specific ingestion rate) yields greater Hg_{ss}, the opposite of SGD (Figure 2b). The effect of increasing growth efficiency on Hg_{ss} depends on both K_e (the efflux rate) and SIR. For a K_e of 0.008, as we estimated for underyearling Atlantic salmon, increasing the growth efficiency from 10% to

TABLE 1.—Site characteristics and their correlations with Hg concentrations in prey invertebrates and juvenile Atlantic salmon over both study years (2005–2006). In the last four columns, correlation coefficients are given with *P*-values in parentheses; significant correlations ($P < 0.05$) are in bold italics.

			Prey Hg		Salmon Hg	
Site characteristic	Mean (SD)	Range	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)

60% yields a 2.0-fold (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} closely matches our empirical observations when bounded by the range of literature estimates of SIR and growth efficiency (compare Figures 1 and 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, the Hg concentration in prey was the most important predictor of that in fish, accounting for 59% of the explained variation. However, mean individual growth rate accounted for 38% of the explained variation in the mean Atlantic salmon Hg concentration independent of the 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 that 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 probably 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 that higher 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 as they grow (yielding higher Hg concentrations in larger fish), SGD can reduce the Hg concentration in 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

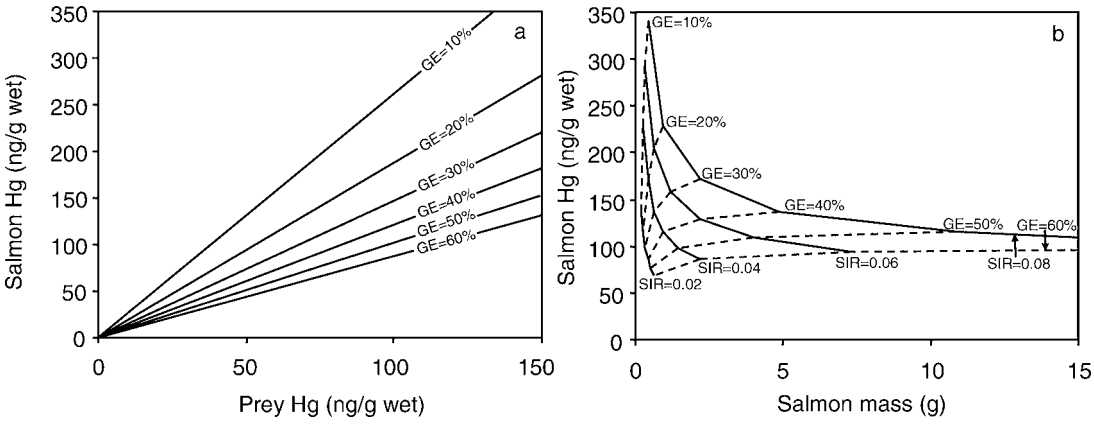

FIGURE 2.—Panel **(a)** shows model-predicted steady-state Hg concentrations in Atlantic salmon for the range of prey Hg concentrations observed in this study with growth efficiency (GE) ranging from 10% to 60% and the ingestion rate (SIR) held constant at 0.08 $g \cdot g^{-1} \cdot d^{-1}$. Panel **(b)** shows model-predicted concentrations for a range of growth rates (size at 100 d) with the variation in growth generated either by varying SIR while holding growth efficiency constant (solid lines) or by varying growth efficiency while holding the consumption rate constant (dashed lines); in both cases the Hg concentration of prey was held constant at 100 ng/g.

efficiency drives the variation in growth rates. We conclude that a suppressed fish growth rate, which is associated with low growth efficiency, increases the susceptibility of fish to Hg contamination.

We used a conservation stocking program for Atlantic salmon as a model system for this study (Folt et al. 1998). The salmon that we sampled were from a protected population and were too small for harvest by humans, although the Hg concentrations that we observed are a potential concern for predators of juvenile salmon (Figure 1). However, our finding that stocked juvenile fish rapidly accumulate Hg in accordance with the site-specific drivers of Hg accumulation is directly relevant to Hg monitoring programs. State and federal agencies stock millions of fish in U.S. lakes and streams each year (Trout Unlimited 1998; Caudill 2005), many as juveniles that will undergo substantial growth and thus have the potential for a good deal of mercury accumulation before reaching harvestable size. With coordination of stocking efforts across targeted sites, measuring the Hg concentration in stocked fish allows for a sampling design in which the species, age, exposure time, and initial Hg concentrations of fish are all standardized across sites. Other systems in which small, juvenile fish are stocked and grow to harvestable size in areas with no natural reproduction are also ideal for this approach (i.e., put–grow–take fisheries), including many North American fisheries for walleyes *Sander vitreus* (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 developing consumption advisories that protect human health (Lepak et al. 2009b).

While prey Hg concentrations clearly drive those in fish, Hg levels in prey may not be amenable to short-term, local control. Thus, clarifying the importance of SGD in determining fish Hg concentrations is important, particularly because the growth of fish is highly variable (more than 10-fold in this study) and sensitive to anthropogenic impacts and fisheries management (Verta 1990; Essington and Houser 2003; Surette et al. 2003). In many fisheries, high stocking density leads to suppressed fish growth rate owing to density-dependent growth, which could exacerbate Hg accumulation. We observed that high stocking density led to suppressed growth of Atlantic salmon, but the effect of stocking density was very small relative to that of prey biomass (Ward et al. 2009) and increased stocking density did not lead to significantly increased Hg concentrations in the fish. However, other studies have shown that intensive fishing to reduce fish population density can lead to higher growth rates and lower 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 to maximize fish growth rates, which could reduce Hg accumulation. The implications for Hg concentrations in harvested fish remain unknown, however.

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

Although both prey Hg concentration and individual growth directly affect the Hg concentration in fish, these factors are themselves controlled by the biotic and abiotic characteristics of the local environment. We found higher Hg concentrations in prey—and consequently higher concentrations in fish—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 concentrations in the biota at sites with more wetland area in the catchment. Wetlands are potentially important sites for the conversion of inorganic Hg to MeHg and thus sources of MeHg for downstream ecosystems, particularly during runoff episodes. However, recent studies indicate that there may be substantial production of MeHg in stream sediments during the growing season (Schuster et al. 2008), and this may be a more important, continuous source of MeHg for stream-dwelling organisms than periodic fluxes from upstream wetlands.

Our findings extend some key patterns identified in studies of Hg accumulation in freshwater lakes to stream systems. In particular, Hg concentrations in lake fish and their invertebrate prey are 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 that we observed in streams, with higher Hg concentrations 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 greater algal biomass (bloom dilution) and prey biomass, along with individual SGD in primary consumers, leads to reduced Hg concentrations 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 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), leading to higher Hg concentrations in prey and confounding the apparent effects of bloom dilution and higher prey biomass across our study streams. In addition, fish grew more slowly at sites with low prey biomass (Ward et al. 2009), so reduced SGD also contributed to the higher Hg concentrations in the fish at these sites. Thus, while this study clearly demonstrates the important direct role of prey Hg concentration and growth in determining the Hg concentrations in stream fish, future research should determine how correlated biotic and abiotic environmental factors drive the variation in prey Hg concentration, fish growth, and growth efficiency and thus the Hg accumulation in fish.

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