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# Manipulation of growth to reduce mercury concentrations in sport fish on a whole-system scale 

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#### Abstract

Altering food web structure has been shown to influence mercury ( Hg ) concentrations in sport fish. Here, we describe a whole-system manipulation designed to assess the effectiveness of stocking relatively high-quality, low- Hg prey (rainbow trout, Oncorhynchus mykiss) as a means of increasing northern pike (Esox lucius) growth to reduce Hg concentrations. A replicated pond experiment served as a reference for the lake experiment and provided information to parameterize bioenergetics simulations. Results indicate that stocking relatively high-quality, low- Hg prey is a rapid and effective method to reduce sport fish Hg concentrations by up to $50 \%$ through an increase in individual northern pike biomass. Large northern pike, the fish that tend to be the most contaminated, were affected most by the manipulation. The observed declines in northern pike Hg concentrations indicate that stocking might be used to reduce Hg concentrations in sport fish prior to harvest. However, after 1 year, northern pike Hg concentrations rebounded, suggesting that reductions would be temporary without continuous stocking. Thus, perhaps the most effective method of perpetually reducing sport fish Hg concentrations would be to manage for the development of a naturally reproducing forage fish population with relatively high energy content and low Hg concentrations.

Résumé : On a démontré que la modification du réseau alimentaire influence les concentrations de mercure ( Hg ) chez les poissons d'intérêt sportif. Nous décrivons ici une manipulation à l'échelle du système entier destinée à évaluer l'efficacité d'un empoissonnement de truites arc-en-ciel (Oncorhynchus mykiss) de qualité relativement élevée se nourrissant de proies à faible teneur en Hg comme moyen d'augmenter la croissance des grands brochets (Esox lucius) afin de réduire leur concentration de Hg. Une expérience conduite en double en étang a servi de témoin pour l'expérience en lac et a fourni les renseignements nécessaires pour déterminer les paramètres des simulations bioénergétiques. Les résultats indiquent que l'empoissonnement de poissons de qualité relativement élevée et à proies à faible teneur en Hg est une méthode rapide et efficace de réduire les concentrations de Hg chez les poissons sportifs de jusqu'à $50 \%$, par le moyen d'une augmentation de la biomasse individuelle des grands brochets. Les grands brochets de taille supérieure, soit les poissons qui ont tendance à être le plus contaminés, sont les plus affectés par la manipulation. Les déclins observés dans les concentrations d'Hg chez le grand brochet indiquent que l'empoissonnement peut servir à réduire les concentrations d'Hg chez les poissons sportifs avant la récolte. Cependant, après une année, les concentrations d'Hg chez le grand brochet remontent, indiquant que les réductions seraient temporaires sans un empoissonnement continu. Ainsi, la méthode la plus efficace de réduire de manière permanente les concentrations d'Hg chez les poissons sportifs serait peut-être d'aménager l'établissement d'une population de poissons fourrage à relativement fort contenu énergétique et à faible concentration d' Hg qui se reproduirait naturellement.


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## Introduction

Mercury $(\mathrm{Hg})$ contamination in fish is a worldwide concern to human and ecosystem health (Bodaly et al. 1993; Johnston et al. 2003; Kamman et al. 2005). Recently, the potential health risks associated with consumption of high-Hg protein sources have become more widely appreciated; however, the health benefits associated with eating fish may potentially offset these risks (Knuth et al. 2003; Institute of Medicine of the National Academies 2007; Mergler et al. 2007). By better understanding and potentially manipulating the processes through which Hg bioaccumulation occurs in fish, it may be possible to maintain the benefits associated with fish consumption while reducing the risks associated with Hg contamination.

A host of factors influence Hg bioaccumulation in individual fish, including size, age, diet, condition, and trophic position (Power et al. 2002; Johnston et al. 2003; McIntyre and Beauchamp 2007). Particularly high levels of Hg tend to occur in large, slow-growing predatory sport fish, which occupy high trophic positions in aquatic food webs (Bahnick et al. 1994; Power et al. 2002). It is known that Hg bioaccumulation in fish results from the assimilation of Hg from their food (Hall et al. 1997) and that Hg concentrations may be altered in fish by changing their diet, metabolism, or growth rate (Harris and Bodaly 1998; MacRury et al. 2002; Trudel and Rasmussen 2006). These findings suggest that decreasing Hg concentrations in fish may be possible using management strategies that alter fish community structure and food web linkages.

Many fishery management strategies, including some stocking and harvest regulations, are aimed at altering fish density, growth, size and age structure, and community structure (Heidinger 1999; Ney 1999; Noble and Jones 1999). Such manipulations can affect Hg concentrations in fish. For example, removal of approximately $90 \%$ of the northern pike (Esox lucius; $>65 \mathrm{~cm}$ total length, TL) from a 120 ha study lake resulted in increased growth and a concurrent $50 \%$ decrease in total mercury ( $\mathrm{T}-\mathrm{Hg}$ ) concentration of the remaining northern pike 2 years after the removal (Sharma et al. 2008). Reduced Hg concentrations arising from increased growth has been termed "growth dilution" (Verta 1990). Growth dilution occurs when growth rate exceeds contaminant uptake rate (Chen and Folt 2005; Ward et al. 2010) and may result from lower foraging activity costs, relatively low Hg concentrations in available prey, and (or) higher food availability or quality (Verta 1990). Stocking prey fish can affect Hg concentrations in much the same way as predator removals. Specifically, stocking relatively high-energy prey fish with relatively low T-Hg concentrations can increase predator growth while limiting Hg intake, resulting in growth dilution in piscivores. While modeling has demonstrated the potential efficacy of fishery management to promote growth dilution of contaminants (Stow et al. 1995), few studies have evaluated the prospects experimentally at the whole-system scale. The mechanisms behind growth dilution (i.e., the importance of growth efficiency, the energy density of prey items, and the Hg concentrations of prey items) can vary depending on the conditions under which it occurs (Verta 1990; Lepak et al. 2009; Ward et al. 2010).

In this study we evaluated the effect of a common manage-
ment strategy on $\mathrm{T}-\mathrm{Hg}$ concentrations of northern pike, a popular piscivorous sport fish. A whole-system manipulation was conducted to evaluate the effects of stocking rainbow trout (Oncorhynchus mykiss) as prey for northern pike to reduce Hg concentrations. A pond experiment was conducted concurrently to replicate the whole-system manipulation. In addition, an attempt was made to evaluate the effects of density reduction on northern pike $\mathrm{T}-\mathrm{Hg}$ concentrations at the pond scale, but small sample size (only six replicate ponds were available) precluded statistical comparisons. Inference was strengthened by examining repeated measures of $\mathrm{T}-\mathrm{Hg}$ concentrations in individual northern pike before and after experimental manipulations at the whole-system and pond scales. Lastly, we used a bioenergetics modeling approach to evaluate the mechanisms behind the observed response to the experimental manipulations.

## Materials and methods

## Site descriptions

The whole-system manipulation was performed at College Lake, a shallow ( 6 m maximum depth) 25 ha reservoir located on the Foothills Research Campus ( 1525 m elevation) of Colorado State University (CSU, Fort Collins, Colorado). It serves primarily as irrigation storage for university grounds. Typically, it is ice-covered from November to late February or early March. The reservoir is nearly isothermal in spring, warming to about $15{ }^{\circ} \mathrm{C}$ by mid-May. The fish assemblage includes northern pike, largemouth bass (Micropterus salmoides), smallmouth bass (Micropterus dolomieu), yellow perch (Perca flavescens), walleye (Sander vitreus), white crappie (Pomoxis annularis), black crappie (Pomoxis nigromaculatus), bluegill (Lepomis macrochirus), and common carp (Cyprinus carpio). Catch-and-release fishing is allowed for 1 day per year during an annual spring tournament (500 angler hours) hosted by the American Fisheries Society student subunit.

Northern pike have dominated the sport fish community in College Lake since 1973 (Willis et al. 1984). Other top piscivores are much less abundant, with catch rates of largemouth and smallmouth bass being second. Density of large ( $\geq 550 \mathrm{~mm}$ total length, TL) northern pike has increased from $7 \pm 6$ fish $\cdot h^{-1}$ ( $95 \%$ confidence interval, CI) in the 1970s (Willis et al. 1984) to $17 \pm 8$ fish $\cdot \mathrm{ha}^{-1}(95 \% \mathrm{CI})$ in spring 2007 and 2008, respectively. Density of northern pike vulnerable to sampling ( $\geq 350 \mathrm{~mm}$ TL) was estimated at $36 \pm$ 11 fish $\cdot \mathrm{ha}^{-1}$ ( $95 \%$ CI) in 2007 and $45 \pm 18$ fish $\cdot \mathrm{ha}^{-1}$ ( $95 \%$ CI) in 2008. Despite a doubling in population density of large northern pike, standing-stock biomass remained relatively static over this time period. Mean mass of individuals $\geq 550 \mathrm{~mm}$ has diminished from 2.7 kg in 1980 (Willis et al. 1984) to $1.2 \pm 1.3 \mathrm{~kg}$ (mean $\pm$ standard deviation, SD ) in 2008. Relatively small individuals ( $350-650 \mathrm{~mm}$ ) currently dominate the population (mean proportional size distribution $=63$; Guy et al. 2007), with few fish exceeding 750 mm . The basin morphology of College Lake is characteristic of small lakes in Minnesota and Wisconsin, which generally contain populations of northern pike that exhibit high densities of slow-growing individuals (Pierce et al. 2003; Pierce and Tomcko 2005; Margenau et al. 2008), and the density and size structure of northern pike in College

Lake are indicative of what is considered to be a "stunted" population (Margenau et al. 2008). In College Lake, northern pike achieve a size preferred by anglers ( 710 mm TL; Anderson and Neumann 1996) in 8-10 years. This growth rate is relatively low when compared with that of other northern pike populations in high plains reservoirs of Colorado (northern pike achieve 710 mm TL in 5-8 years), particularly those where growth is continuously supplemented with stocked rainbow trout (Rogers et al. 2005), and when compared with the growth rate of reference populations across the range of the species (achieve 710 mm TL in $7-8$ years; Casselman 1996).

The pond experiment was conducted at the CSU Foothills Fisheries Laboratory, about 0.6 km from College Lake. Six ponds (approximately 0.1 ha with a maximum depth of 1.5 m ) were prepared for the experiment by clearing the banks and pond bottoms of large vegetation. Two aeration stones were added to each pond to supply oxygen. The ponds were filled with water from College Lake in early March 2009, and additional water was added as needed to offset evaporation and infiltration losses.

## Pre-treatment sampling and setup

Northern pike $(n=250)$ were collected from College Lake by angling, gill netting, boat electrofishing, and trap netting from 7 to 15 March 2009. The fish were anesthetized using a $25 \mathrm{mg} \cdot \mathrm{L}^{-1}$ solution of tricaine methanesulfonate (MS-222). Each fish was measured (TL, mm) and weighed (g) after removing stomach contents by gastric lavage. Stomach contents were fixed in $10 \%$ neutral buffered formalin for later identification. Muscle tissue was collected from the anterior-dorsal musculature of every individual using a 3.5 mm biopsy needle sterilized in a $90 \%$ isopropyl alcohol solution. Each sample was placed into an individually labeled microcentrifuge tube and stored at $-20^{\circ} \mathrm{C}$. A $1: 1$ mixture of denture adhesive and antibiotic ointment was used to treat the biopsy wound. Northern pike were individually marked using a Floy tag, if not already present, and released. Fish were returned to College Lake ( 230 fish; mean $\mathrm{TL} \pm \mathrm{SD}=545 \pm 64 \mathrm{~mm}$; mean mass $\pm \mathrm{SD}=912 \pm 392 \mathrm{~g}$ ) or stocked into the ponds (20 fish; mean TL $\pm \mathrm{SD}=570 \pm 44 \mathrm{~mm}$; mean mass $\pm \mathrm{SD}=$ $1034 \pm 392 \mathrm{~g}$ ) for later resampling.

Representative samples of fish and invertebrate prey of northern pike were collected by hand, gill netting, and seining in College Lake in March 2009 and from the ponds after draining in May 2009 (Appendix A, Table A1). Prey were measured, weighed, and stored at $-20^{\circ} \mathrm{C}$ for subsequent Hg analyses. These collections served to qualitatively compare northern pike Hg exposure from their prey items in the reservoir and pond environments.

On 15 March 2009, 20 northern pike (mean TL $\pm$ SD $=$ $570 \pm 44 \mathrm{~mm}$ ) sampled from College Lake, and processed as described previously, were stocked in the ponds. Two ponds were stocked with northern pike densities equivalent to that of the study reservoir ( 45 fish $\cdot \mathrm{ha}^{-1}$ or 4 fish $\cdot$ pond $^{-1}$ ). Two ponds were stocked with half the density of northern pike as the study reservoir (two fish each). The remaining two ponds were stocked with the same northern pike density as in the study reservoir (four fish each) and subsidized with rainbow trout as prey.

Rainbow trout, averaging 150 mm TL (ranging from $\sim 100$
to 200 mm ) and 39 g (ranging from $\sim 10$ to 100 g ) (Appendix A, Table A1), were provided by the Colorado Division of Wildlife Bellvue-Watson Fish Hatchery. Northern pike can consume prey up to $50 \%$ of their own body length (Mittelbach and Persson 1998), so the smallest northern pike used in this study had access to prey ranging from 0 to 229 mm , which included all stocked rainbow trout, while the largest pike had access to prey ranging from 0 to 354 mm . Prior to stocking, 15 rainbow trout over a range of sizes were measured, weighed, and frozen at $-20^{\circ} \mathrm{C}$ for subsequent Hg analyses. On 19 March 2009, approximately 9000 rainbow trout ( $\sim 350 \mathrm{~kg}$ ) were stocked into College Lake and approximately $100(4 \mathrm{~kg})$ in each of the two treatment ponds containing four northern pike ( $\sim 20 \mathrm{~kg}$ ) as supplemental prey. The other four ponds did not receive rainbow trout as supplemental prey. On 30 March 2009, another 17000 rainbow trout ( $\sim 650 \mathrm{~kg}$ ) were stocked into College Lake. The experimental stocking rate was approximately double that of a nearby large ( $\sim 450 \mathrm{ha}$ ) reservoir and similar to that of other smaller systems ( $\sim 50-100 \mathrm{ha}$ ) in Colorado. The total biomass stocked was equivalent to about 1 kg of rainbow trout per northern pike in both College Lake and in the two subsidized ponds.

## Monitoring and post-treatment sampling

Our intention was to conclude the experiments in the reservoir and ponds when the northern pike had exhausted their supplemental prey supply. We assumed that northern pike could digest approximately $3.25 \%$ of their body mass in rainbow trout per day (Nilsson and Brönmark 2000). Given that about 1000 northern pike weighing an average of 1 kg each were in the study reservoir, we estimated that this population would consume all the stocked rainbow trout in approximately 31 days. Because other piscivores were present in College Lake (avian and piscine) and the ponds (avian), and rainbow trout likely had some level of predator avoidance, we monitored the ponds two to three times weekly for evidence of rainbow trout (i.e., surface feeding). Rainbow trout activity was greatly reduced by 27 April 2009, and the pond experiment was terminated 1 May 2009, 44 days after the manipulation began. The whole-system experiment was concluded 8-9 May 2009, when northern pike were recaptured, 51-52 days after the manipulation began.

We recaptured 30 tagged northern pike from College Lake and 20 northern pike from the ponds; these fish had been biopsied and released prior to the start of the manipulations. Approximately 1 year later ( 15 May 2010), we recaptured another 15 tagged northern pike from the reservoir to evaluate the long-term response to the manipulation. All these fish were euthanized with an overdose of MS-222. Stomach contents were removed and fixed in $10 \%$ neutral buffered formalin. Fish were measured and weighed, and a sample of muscle tissue was collected for Hg analysis using the same procedure as in the pre-treatment sampling.

## Diet and mercury analyses

Diet composition, expressed as a percentage by wet mass, was estimated for northern pike before (College Lake) and after (College Lake and the ponds) the manipulations. Prey were identified to the lowest taxonomic level feasible: order for aquatic insects, genus for crayfish (Orconectes spp.), and species for vertebrates. Head capsule widths (nearest 0.1 mm )
were used to estimate wet mass of insects using relationships in the literature (Smock 1980; Benke et al. 1999). Crayfish carapace lengths (Roell and Orth 1992) or chelae widths (J.M. Lepak, unpublished data) were used to estimate wet mass. Prey fish wet mass was obtained from mass-length relationships (B.M. Johnson, unpublished data). When only a partial backbone was available for analysis, vertebrae were measured and enumerated. The partial backbone length was divided by the ratio of partial to complete vertebral count (known for each species), and the resulting complete backbone length was used to compute the wet mass of the fish. Frogs and a single bird were weighed whole when diets were analyzed, since little digestion had occurred and the samples were frozen and not fixed in formalin.

All organisms collected for Hg analyses were analyzed on a wet mass basis, with the exception of northern pike biopsied muscle tissue, which was dried for 72 h at $60^{\circ} \mathrm{C}$ prior to $\mathrm{T}-\mathrm{Hg}$ analysis. This was done to reduce error associated with high surface area to volume ratios influencing the ratio of wet mass / dry mass and, subsequently, Hg concentrations. This was necessary because of the low mass associated with biopsy samples required for nonlethal tissue collection. Northern pike tissue samples were tested for $\mathrm{T}-\mathrm{Hg}$ before and after the experimental manipulation.

Whole prey organisms collected from the ponds were analyzed for Hg concentrations when possible. Because we wanted the Hg concentrations in the prey in our study system to be comparable with data from the Colorado Department of Public Health and Environment, skinless and exoskeletonfree muscle tissue samples from hatchery-raised rainbow trout, prey fish, and crayfish collected from College Lake were analyzed for Hg concentrations.

All fish samples were tested for $\mathrm{T}-\mathrm{Hg}$ as a surrogate for methylmercury ( MeHg ), assuming $\mathrm{T}-\mathrm{Hg}$ was composed of $\geq 95 \% \mathrm{MeHg}$ (Bloom 1992). Invertebrate samples and frog muscle tissue samples were analyzed for MeHg and inorganic Hg . All Hg analyses were conducted by Quicksilver Scientific (Lafayette, Colo., USA). Reference materials of known inorganic Hg and MeHg concentrations, including BCR 463 (tuna fish) and DOLT-3 (dogfish liver tissue), were used as quality controls. Samples tested for $\mathrm{T}-\mathrm{Hg}$ (detection limit $=$ 10-30 $000 \mathrm{ng} \cdot \mathrm{g}^{-1}$ ) were analyzed with a NIC MA-2000 (Nippon Instrument Corporation, Osaka, Japan) by combustion (EPA Method 7473). Percent recoveries of reference materials (BCR 463, $n=11$; DOLT-3, $n=19$ ) for T-Hg ranged from $88.0 \%$ to $108.0 \%$, with a mean $\pm$ SD of $98.3 \% \pm 5.6 \%$. Duplicate samples for $\mathrm{T}-\mathrm{Hg}(n=12)$ had a percent deviation ranging from $0.1 \%$ to $11.5 \%$, with a mean $\pm \mathrm{SD}$ of $6.2 \% \pm$ $3.9 \%$. Samples tested for Hg speciation (detection limit $=$ $0.05-10000 \mathrm{ng} \cdot \mathrm{g}^{-1}$ ) were analyzed using an ion chromatographic separation of cationic Hg -thiourea complexes, followed by sequential oxidation of $\mathrm{CH}_{3} \mathrm{Hg}^{+}$to $\mathrm{Hg}^{\text {II }}$, stannous chloride reduction of $\mathrm{Hg}^{\text {II }}$ to $\mathrm{Hg}^{0}$, evaporation of $\mathrm{Hg}^{0}$ into an Ar carrier, drying of the sample gas, and finally atomic fluorescence detection. For further details about this method, see Shade and Hudson (2005) and Shade (2008). Percent recoveries of reference materials for MeHg (BCR 463, $n=1$; DOLT- $3, n=1$ ) were $97.0 \%$ and $100.1 \%$, respectively. Percent recoveries of reference materials for inorganic Hg (BCR $463, n=1$; DOLT- $3, n=1$ ) were $101.1 \%$ and $103.5 \%$, respectively. Duplicate samples for $\mathrm{MeHg}(n=2)$ had percent
deviations of $1.1 \%$ and $2.2 \%$, with a mean $\pm$ SD of $1.65 \% \pm$ $0.78 \%$. Duplicate samples for inorganic $\mathrm{Hg}(n=2)$ were both below detection levels.

## Statistical analyses

Comparisons between individual northern pike mass and $\mathrm{T}-\mathrm{Hg}$ concentration prior to and approximately 50 days after the experimental manipulation began were conducted using SAS Proc Mixed (SAS Institute Inc. 2009-2010). Changes in mass and $\mathrm{T}-\mathrm{Hg}$ concentration as a result of the experimental manipulation in College Lake were analyzed using a onefactor repeated measures analysis of variance (RM ANOVA), with either mass or $\mathrm{T}-\mathrm{Hg}$ concentration used as the factor ( $n=29$; one pre-manipulation sample was mishandled during analysis). Sampling period was defined as the fixed effect and individual as the random effect. One-factor RM ANOVA analyses, with mass and $\mathrm{T}-\mathrm{Hg}$ concentration as the factors, were also used to compare mass and $\mathrm{T}-\mathrm{Hg}$ concentration prior to and approximately 1 year after the experimental manipulation in College Lake ( $n=15$ ). Sampling period was defined as the fixed effect and individual as the random effect. Values were reported from the type III test of fixed effects for each analysis.

In the pond experiment, small sample sizes precluded statistically valid comparisons between unfed northern pike from ponds of differing densities. Thus, data from ponds stocked with northern pike at the same density as the study reservoir and half the density of the study reservoir were combined into a group termed "unfed" for all comparisons. A one-factor RM ANOVA analysis, with either mass or T-Hg concentration as the factor, was used to compare changes in mass and T-Hg concentration within the unfed $(n=12)$ and increased prey ( $n=7$; one pre-manipulation sample was mishandled during analysis) treatments. Sampling period was defined as the fixed effect and individual as the random effect. Values were reported from the type III test of fixed effects.

Linear regression analyses, conducted using SAS Proc Reg (SAS Institute Inc. 2009-2010), were used to analyze the relationship between individual northern pike initial length and the proportional change in individual northern pike mass in College Lake $(n=29)$ and the ponds $(n=19)$ at the end of the experiment. In addition, linear regression analyses were used to analyze the relationship between the proportional change in individual northern pike mass and the proportional change in their $\mathrm{T}-\mathrm{Hg}$ concentration in both College Lake $(n=29)$ and the ponds $(n=19)$. For the pond data, individual northern pike responses were pooled across all ponds prior to performing linear regression analyses. The slope and intercept of the College Lake and pond data trend lines, describing the relationship between the proportional change in individual northern pike mass and the proportional change in their T-Hg concentration, were compared using a two-factor analysis of covariance (ANCOVA) in SAS Proc GLM (SAS Institute Inc. 2009-2010). Proportional mass change and experiment locations were used as the two factors to determine whether the responses to the experimental manipulations were similar.

The assumption of normality, tested using a Shapiro-Wilk test in SAS Proc Capability test (SAS Institute Inc. 20092010), was met by the College Lake northern pike mass data
( $n=29, W=0.97, p=0.57$ ), the College Lake T- Hg data ( $n=29, W=0.97, p=0.57$ ), the pond northern pike mass data ( $n=19, W=0.96, p=0.70$ ), and the pond T-Hg data ( $n=19, W=0.91, p=0.08$ ); thus, no transformations were performed on the data prior to analyses.

## Bioaccumulation model

We used data obtained from this project and the literature to develop a bioenergetics model coupled with a bioaccumulation model to predict northern pike Hg concentrations. We then used these simulations to provide insight into the mechanisms driving the empirical results observed. Daily northern pike Hg accumulation was calculated using estimated consumption of prey species from Fish Bioenergetics 3.0 (Hanson et al. 1997) coupled with the mass balance model developed by Trudel and Rasmussen (1997) using the following equation:

$$
\begin{equation*}
\mathrm{Hg}_{\mathrm{NPK}}=\left(\alpha \times C \times \mathrm{Hg}_{\text {prey }}\right)-E \tag{1}
\end{equation*}
$$

where $\mathrm{Hg}_{\text {NPK }}$ is northern pike Hg uptake $(\mu \mathrm{g})$, $\alpha$ is the assimilation efficiency of prey $\mathrm{Hg}, C$ is daily consumption of a given prey item in grams, $\mathrm{Hg}_{\text {prey }}$ is the northern pike prey item Hg concentration ( $\mu \mathrm{g} \cdot \mathrm{g}^{-1}$ ), and $E$ is the daily elimination of $\mathrm{Hg}(\mu \mathrm{g})$. The assimilation efficiency of Hg was assumed to be 0.8 , reflecting the assimilation efficiency of sulfurcontaining proteins to which Hg is covalently bound (Brett and Groves 1979; Harris et al. 2003; Trudel and Rasmussen 2006). Daily Hg uptake was added to the initial northern pike Hg body burden (mean of northern pike in the ponds stocked with rainbow trout), and whole-body Hg concentration was then calculated by dividing these values for every day of the simulation by the estimated daily mass of the fish (g).

Daily elimination of $\mathrm{Hg}(E)$ was calculated using the equation developed by Trudel and Rasmussen (2001):

$$
\begin{equation*}
E=\phi \times M^{\beta} \times \mathrm{e}^{\gamma T} \tag{2}
\end{equation*}
$$

where $E$ is the daily elimination of $\mathrm{Hg}(\mu \mathrm{g}), \phi$ is the coefficient of Hg elimination, $M$ is northern pike mass $(\mathrm{g}), \beta$ is the allometric exponent of Hg elimination, $\gamma$ is the temperature coefficient of Hg elimination, and $T$ is water temperature $\left({ }^{\circ} \mathrm{C}\right)$. The coefficient of Hg elimination, the allometric exponent of Hg elimination, and the temperature coefficient of Hg elimination were set to $0.0029,-0.20$, and 0.066 , respectively (Trudel and Rasmussen 1997).

Default northern pike physiological parameter settings were used in all simulations (Hanson et al. 1997). Daily water temperatures were derived from the means of midwater column temperatures taken throughout the experiment every 3 h in the ponds stocked with rainbow trout. We varied northern pike growth, prey Hg concentration, and prey energy density. Northern pike growth was simulated as high (mean growth of northern pike from the experimental ponds stocked with rainbow trout) or low (no net change in mass). We characterized low growth as no net change in mass because we observed individual northern pike in College Lake that lost or did not change mass over the course of the 5152 day manipulation. Additionally, northern pike that did not have access to rainbow trout in the ponds showed no significant change in mass. Prey Hg concentrations were either high
(the mean crayfish Hg concentration in College Lake) or low (the mean rainbow trout Hg concentration at stocking; see Appendix A, Table A1). Finally, prey energy densities were either high (measured rainbow trout energy density) or low (crayfish energy density determined from the literature; see Results). A final simulation was run to estimate the maximum reduction rate in northern pike Hg concentration when net fish mass did not change. For this simulation, northern pike consumed a maintenance ration with prey Hg concentration set to zero, so additional Hg exposure was zero. All simulations were run for 44 days to mimic the pond experiments.

## Results

## Response to the whole-lake manipulation

Diets of individual northern pike in College Lake varied little, but prey types varied in energy density. Prior to rainbow trout stocking, northern pike diets $(n=250)$ in College Lake consisted almost entirely of crayfish and few prey fish (Fig. 1). At the initial recapture event (51-52 days later), northern pike diets $(n=30)$ consisted primarily of crayfish and prey fish, with less than $25 \%$ of the diets consisting of rainbow trout, indicating that some rainbow trout remained in College Lake. Northern pike diets from fish recaptured in May $2010(n=15)$ consisted largely of crayfish and a few prey fish, as they had prior to rainbow trout stocking in 2009 (Fig. 1). Hatchery-reared rainbow trout had energy densities of approximately $5702 \mathrm{~J} \cdot(\mathrm{~g} \text { wet mass) })^{-1}$ (J.M. Lepak, unpublished data), while crayfish have energy densities of approximately $3088 \mathrm{~J} \cdot(\mathrm{~g} \text { wet mass) })^{-1}$ (King and Ball 1967; Kelso 1973; Probst et al. 1984), and the other prey fish sampled have energy densities of approximately $4186 \mathrm{~J} \cdot(\mathrm{~g}$ wet mass) ${ }^{-1}$ (Hanson et al. 1997).

The introduction of rainbow trout resulted in a shift in College Lake northern pike ( $n=29$ ) masses and T-Hg concentrations measured 51-52 days after stocking. Initially, individual northern pike that were later recaptured for analysis $(n=29)$ weighed an average of $999 \pm 325 \mathrm{~g}$ (mean $\pm$ SD; all values reported in the Results are means $\pm$ SD). There was a significant increase in individual northern pike mass during the manipulation (RM ANOVA; $n=29, F=35.51$, $p<0.01$ ), with mean mass increasing to $1146 \pm 430 \mathrm{~g}$. This corresponded to a mean mass gain of approximately $15 \%$. For comparison, individual northern pike $\geq 500 \mathrm{~mm}$ ( $n=$ 18) captured, weighed, and marked between 21 and 31 March 2007 that were recaptured on 14 April 2007 gained an average of $3 \%$ of their body mass, and individual northern pike $\geq 500 \mathrm{~mm}(n=9)$ captured, weighed, and marked between 9 March and 9 April 2008 that were recaptured on 26 April 2008 lost an average of $12 \%$ of their body mass (A.G. Hansen, unpublished data). In this experiment we also observed a significant positive relationship between initial length of individual northern pike and their proportional mass change during the experimental manipulation (linear regression; $n=29, F=22.23, p<0.01, R^{2}=0.41$; Fig. 2).

The observed shift in mass of the northern pike after stocking rainbow trout corresponded with changes in their $\mathrm{T}-\mathrm{Hg}$ concentrations. Concentrations of $\mathrm{T}-\mathrm{Hg}$ in northern pike were significantly lower at the end of the experiment (RM ANOVA; $n=29, F=17.11, p<0.01$ ), decreasing from $2142 \pm 860 \mathrm{ng} \cdot(\mathrm{g} \text { dry mass })^{-1}$ prior to the experimental ma-

Fig. 1. Diet composition (by percentage of wet biomass) of northern pike (Esox lucius) from College Lake and the experimental ponds for each sampling occasion. Percent biomass of crayfish (Orconectes spp.), other invertebrates, rainbow trout (Oncorhynchus mykiss), and other fish are represented with solid white, dark grey, black, and light grey bars, respectively. Percent biomass of chorus frogs (Pseudacris sp.) and the yellow-rumped warbler (Dendroica coronata) are represented with vertically and horizontally hatched bars, respectively. Samples sizes of northern pike are shown at the bottom of each bar. Samples designated as initial capture, initial recapture, and recapture (2010) were samples collected from College Lake. Samples designated as unfed and increased forage were samples collected from the experimental ponds.


Fig. 2. Individual proportional mass change as a function of total length for the 29 northern pike (Esox lucius) resampled from College Lake immediately following the experimental manipulation.

nipulation, to $1726 \pm 473 \mathrm{ng} \cdot(\mathrm{g} \text { dry mass })^{-1}$ after the experimental manipulation. A significant negative relationship was observed between individual northern pike mass change and the proportional change in their $\mathrm{T}-\mathrm{Hg}$ concentration (linear regression; $n=29, F=17.06, p<0.01, R^{2}=0.39$ ), with

T- Hg of the most contaminated fish dropping by almost $50 \%$ (Fig. 3).

## Responses to the pond manipulations

Northern pike diet in the ponds was constrained by the

Fig. 3. Proportional change in total mercury ( $\mathrm{T}-\mathrm{Hg}$ ) concentration of individual northern pike (Esox lucius) immediately following the experimental manipulation as a function of proportional mass change in College Lake (filled boxes) and the ponds (triangles). Open and dark grey triangles represent fish from the unfed ponds with four and two fish per pond, respectively. The light grey triangles represent fish from the ponds where rainbow trout (Oncorhynchus mykiss) were stocked.

controlled conditions. In the unfed treatments, at the conclusion of the experiment, diets $(n=12)$ consisted of mostly chorus frogs (Pseudacris sp.), with some Anisoptera larvae (Fig. 1). In the increased prey treatments, rainbow trout were found in the stomachs of a portion of the northern pike at the end of the experiment, accounting for $99 \%$ of the stomach contents of those fish ( $n=8$; Fig. 1). Upon draining the ponds after the completion of the experiment, five researchers searching intensively found only a single rainbow trout in the treatment ponds, suggesting that few remained.

Northern pike responded differently to the two treatments (unfed versus increased prey) in the pond experiment, with regard to both mass and $\mathrm{T}-\mathrm{Hg}$ concentration. In the unfed treatments, individual northern pike mass did not change significantly ( $1057 \pm 260 \mathrm{~g}$ before versus $1005 \pm 242 \mathrm{~g}$ ) during the experimental manipulation (RM ANOVA; $n=12, F=$ 3.15, $p=0.10$; Table 1). Additionally, $\mathrm{T}-\mathrm{Hg}$ concentration did not change in the unfed treatments (RM ANOVA; $n=$ $12 ; F=0.99, p=0.34$ ) with a mean initial T-Hg concentration of $1838 \pm 469 \mathrm{ng} \cdot\left(\mathrm{g}\right.$ dry mass) ${ }^{-1}$, and a mean of $1933 \pm$ $529 \mathrm{ng} \cdot(\mathrm{g} \text { dry mass })^{-1}$ at the conclusion of the experiment (Fig. 3; Table 1). In contrast, individual northern pike mass increased significantly ( $972 \pm 145 \mathrm{~g}$ before versus $1167 \pm$ 183 g after) during the experiment in the ponds with increased prey (RM ANOVA; $n=7, F=31.37, p<0.01$; Table 1), indicating that the treatment (providing rainbow trout as forage) was responsible for the differences in northern pike growth in the ponds.

Similar to the results observed from the whole-lake manipulation, the increases in mass observed in northern pike in the increased prey treatments in the ponds corresponded to changes in the their $\mathrm{T}-\mathrm{Hg}$ concentrations. Individual $\mathrm{T}-\mathrm{Hg}$ concentrations decreased significantly immediately after the experimental manipulation in the ponds with increased prey (RM ANOVA; $n=7, F=57.65, p<0.01$ ) from a mean initial T-Hg concentration of $1450 \pm 247 \mathrm{ng} \cdot(\mathrm{g} \text { dry mass })^{-1}$ to a mean $\mathrm{T}-\mathrm{Hg}$ concentration of $1167 \pm 231 \mathrm{ng} \cdot \mathrm{g}$ dry mass $)^{-1}$ (Table 1). Overall, a significant negative relationship was ob-
served between northern pike mass change in the ponds and the proportional change in their $\mathrm{T}-\mathrm{Hg}$ concentration (linear regression; $n=19, F=17.99, p<0.01, R^{2}=0.51$; Fig. 3). No significant relationship was observed between initial length of northern pike in the ponds and their proportional mass change during the experimental manipulation (linear regression; $n=19, F=1.36, p=0.26$ ).

## Long-term response to the manipulation

Over the short-term, T-Hg concentrations of northern pike in College Lake and the experimental ponds displayed similar responses to the stocking of rainbow trout. No significant differences in slopes (ANCOVA; $n=38, F=0.00, p=0.95$ ) or intercepts (ANCOVA; $n=38, F=0.10, p=0.76$ ) were observed between the relationships of northern pike proportional mass change and change in $\mathrm{T}-\mathrm{Hg}$ concentrations across the reservoir and pond experiments immediately following their completion (Fig. 3). However, the effects of introducing high-quality, low- Hg prey on the $\mathrm{T}-\mathrm{Hg}$ concentrations of northern pike were transient. One year after the manipulation, Hg concentrations $\left(1889 \pm 484 \mathrm{ng} \cdot(\mathrm{g} \text { dry mass })^{-1}\right)$ in northern pike from College Lake were significantly higher than their values measured prior to the introduction of rainbow trout (1672 $\pm 552 \mathrm{ng} \cdot(\mathrm{g} \text { dry mass) })^{-1}$; RM ANOVA; $n=15$, $F=9.75, p<0.01$ ). There was a significant increase in individual northern pike masses 1 year after the experimental manipulation (RM ANOVA; $n=15, F=9.87, p=0.007$ ), with mean mass increasing from $844 \pm 216 \mathrm{~g}$ to $913 \pm 170$ g. This was equivalent to a mean northern pike mass gain of $8 \%$ from just prior to the manipulation to approximately 1 year after the manipulation. Thus, the effects of the trout stocking were temporary; once the stocked rainbow trout were depleted, northern pike growth slowed relative to when rainbow trout were available, and northern pike began to bioaccumulate Hg as they had prior to the manipulation (Fig. 4).

## Implications for human health and consumption

The concentration of Hg in fish that triggers a human

Table 1. Pond experiment design and results of two treatments, unfed (no rainbow trout, Oncorhynchus mykiss added) and trout (rainbow trout added).

| Treatment | No. fish <br> per pond | Initial <br> mass $(\mathrm{g})$ | Final <br> mass $(\mathrm{g})$ | Initial Hg <br> $\left(\mathrm{ng} \cdot \mathrm{g}^{-1}\right)$ | Final Hg <br> $\left(\mathrm{ng} \cdot \mathrm{g}^{-1}\right)$ | Pond <br> No. |
| :--- | :--- | ---: | ---: | ---: | :--- | :--- |
| Unfed | 4 | 1045 | 1090 | 3021 | 2665 | 1 |
| Unfed | 4 | 750 | 784 | 1434 | 1328 | 1 |
| Unfed | 4 | 1000 | 1058 | 1535 | 1353 | 1 |
| Unfed | 4 | 1155 | 1017 | 1922 | 1526 | 1 |
| Unfed | 4 | 810 | 740 | 1627 | 1706 | 5 |
| Unfed | 4 | 790 | 710 | 1867 | 2209 | 5 |
| Unfed | 4 | 1290 | 995 | 1460 | 2028 | 5 |
| Unfed | 4 | 1345 | 1254 | 1951 | 2351 | 5 |
| Unfed | 2 | 1305 | 1308 | 1736 | 2135 | 4 |
| Unfed | 2 | 915 | 974 | 1675 | 1644 | 4 |
| Unfed | 2 | 1510 | 1423 | 2422 | 2891 | 6 |
| Unfed | 2 | 775 | 690 | 1410 | 1364 | 6 |
| Trout | 4 | 1170 | 1495 | No data | 1652 | 2 |
| Trout | 4 | 965 | 1022 | 1461 | 1151 | 2 |
| Trout | 4 | 1170 | 1411 | 1646 | 1326 | 2 |
| Trout | 4 | 1085 | 1226 | 1575 | 1436 | 2 |
| Trout | 4 | 910 | 1130 | 1461 | 1042 | 3 |
| Trout | 4 | 805 | 883 | 1289 | 975 | 3 |
| Trout | 4 | 1080 | 1291 | 1726 | 1407 | 3 |
| Trout | 4 | 795 | 1004 | 993 | 832 | 3 |

Note: The number of northern pike (Esox lucius) per pond is either four (similar density as College Lake) or two (half the density of College Lake).

Fig. 4. Post T-Hg concentration versus pre T-Hg concentration of northern pike (Esox lucius) at initial recapture (May 2009; filled boxes) and 1 year after manipulation (May 2010; dark grey triangles) of the College Lake food web structure. The solid line represents the 1:1 line.

health consumption advisory in Colorado is $2000 \mathrm{ng} \cdot(\mathrm{g}$ dry mass) $)^{-1}$ ( 500 ng .(g wet mass) $)^{-1}$, assuming $75 \%$ water content; Hartman and Brandt 1995). Of the 29 northern pike analyzed for T-Hg concentrations in College Lake, $44 \%$ had T-Hg concentrations exceeding 2000 ng .(g dry mass) ${ }^{-1}$ prior to the experimental stocking of rainbow trout. After the experimental stocking of rainbow trout ( $51-52$ days), $\mathrm{T}-\mathrm{Hg}$ concentrations had decreased significantly. Only $31 \%$ of the pike retained THg concentrations greater than the Colorado consumption advisory, with the majority of these having concentrations that were markedly reduced to just above the advisory level (Fig. 5).

## Mechanism underlying observed responses in T-Hg

Simulations predicting T-Hg concentrations indicated that increased growth of northern pike was an important contributor to the reduction in their Hg concentrations. In all simulations where northern pike growth was set to the mean mass gained by fish in the ponds where rainbow trout forage was provided, predicted Hg concentrations were similar to those measured empirically (Fig. 6). In these simulations, switching prey Hg concentrations from high ( $35.5 \mathrm{ng} \cdot \mathrm{g}^{-1}$ ) to low ( $19.3 \mathrm{ng} \cdot \mathrm{g}^{-1}$ ) values and increasing prey energy densities from low ( $3088 \mathrm{~J} \cdot \mathrm{~g}^{-1}$ ) to high ( $5702 \mathrm{~J} \cdot \mathrm{~g}^{-1}$ ) values by the same percentage ( $54 \%$ difference) had the same effect on

Fig. 5. T-Hg concentration versus length of northern pike (Esox lucius) prior to (black diamonds) and after (light grey diamonds) the experimental manipulation, stocking of rainbow trout (Oncorhynchus mykiss) in College Lake and the experimental ponds. The Colorado fish consumption advisory due to Hg contamination is shown as a broken line, assuming all northern pike were $75 \%$ water by mass.


Fig. 6. Bioenergetic simulations estimating northern pike (Esox lucius) Hg concentrations. Simulations represent estimates varying northern pike growth, prey Hg concentration, and prey energy density. The shaded boxes represent low growth, high prey Hg concentration, and low prey energy density (the closest representation of a crayfish diet). The shaded crosses represent low growth, low prey Hg concentration, and low prey energy density. The shaded triangles represent low growth, high prey Hg concentration, and high prey energy density. The shaded diamonds represent low growth, low prey Hg concentration, and high prey energy density. The black dashes represent low growth, zero prey Hg concentration, and both high and low prey energy density. The black boxes represent empirical mean northern pike Hg concentrations. The open diamonds represent high growth, high prey Hg concentration, and low prey energy density. The black crosses represent high growth, high prey Hg concentration, and high prey energy density. The open triangles represent high growth, low prey Hg concentration, and low prey energy density. The open boxes represent high growth, low prey Hg concentration, and high prey energy density (the closest representation of a rainbow trout (Oncorhynchus mykiss) diet).

northern pike Hg concentrations, decreasing them by the same proportion (approximately $1.5 \%$; Fig. 6). Similarly, simulations where northern pike growth rates were set to zero, decreasing prey Hg concentrations and increasing prey energy densities also had the same effect proportionally on northern pike Hg concentrations, increasing them by approximately $1.5 \%$. Hence, there was a high level of overlap of predicted Hg concentrations in these scenarios (Fig. 6). The maximum theoretical reduction in Hg concentrations in northern pike experiencing zero growth (when no Hg was added by prey consumption) was equivalent to the Hg elimi-
nation rate (Fig. 6). Over the 44 day simulation periods, the addition of biomass with Hg concentrations lower than the Hg elimination rate increased the rate of reduction in northern pike Hg concentrations by 2.5 - to 6.7 -fold compared with the maximum theoretical rate of reduction if northern pike did not grow.

## Discussion

In this study, $\mathrm{T}-\mathrm{Hg}$ concentrations in individual northern pike were significantly reduced, resulting from rapid growth
following rainbow trout stocking at the whole-system and pond scales. Northern pike that consumed rainbow trout experienced growth dilution, which has been described previously as a result of predator density reductions (Göthberg 1983; Verta 1990). However, our manipulations might be better characterized as "biomass dilution", since predator Hg concentrations were reduced by the addition of biomass, resulting from an increase in the availability of preferred, relatively high-energy, low-Hg prey items. The results presented here demonstrate effects at the top of food webs when trophic manipulations alter sport fish prey Hg concentration, quality, and abundance. Analogous results at the base of food webs (termed "bloom dilution") occur when Hg concentrations in herbivorous zooplankton are reduced by the consumption of a "bloom" of low Hg and high-energy phytoplankton stimulated by favorable conditions (high nutrient availability) for growth (Pickhardt et al. 2002; Chen and Folt 2005).

Our data suggest that the increased growth and subsequent reduction in northern pike Hg concentrations was a direct result of rainbow trout stocking. We assumed that individual northern pike growth observed immediately following the manipulation ( 8 and 9 May 2009) would be similar to growth observed 1 year later (15 May 2010) if the treatment had no effect at the lake scale. However, we found that individual northern pike masses had increased an average of $15 \%$ immediately following rainbow trout stocking (51-52 days later), while masses had only increased $8 \%$ one year after the manipulation. Additionally, individual northern pike mass gain in College Lake over similar time periods in 2007 and 2008 was low or negative (A.G. Hansen, unpublished data). We also observed that individual northern pike masses in the ponds where rainbow trout were available were significantly higher at the completion of the experiment, while individuals in the ponds where rainbow trout were not available had not changed in mass significantly. Similarly, these results mimicked those observed with respect to Hg concentrations in the lake and ponds, where individual northern pike that had gained mass had significantly reduced Hg concentrations. Thus, using the results from the whole-lake and pond experiments together, we were able to conclude that the treatments were responsible for differences in northern pike growth and Hg concentrations.

We found that introducing relatively high-energy prey species with relatively low $\mathrm{T}-\mathrm{Hg}$ concentrations can result in rapid reductions in $\mathrm{T}-\mathrm{Hg}$ of popular sport fish, reducing the fraction of the population subject to fish consumption advisories. Observational studies (Kidd et al. 1999; Simoneau et al. 2005; Sharma et al. 2008) also indicate the importance of prey density and predator growth rate as moderators of Hg concentrations in piscivorous fish, including northern pike. For example, Sharma et al. (2008) observed that the removal of approximately $90 \%$ of northern pike $>65 \mathrm{~cm}$ TL from their study system increased the growth increment of the northern pike remaining (age-3 fish had mean lengths of $\sim 325 \mathrm{~mm}$ TL before the removal and mean lengths of $\sim 400$ and $\sim 425 \mathrm{~mm}$ TL 1 and 2 years following the initiation of the removal, respectively). This corresponded to a reduction in northern pike Hg concentrations of approximately $50 \%$. The rapid response by northern pike to rainbow trout stocking in our study demonstrates that changes in food web struc-
ture can alter $\mathrm{T}-\mathrm{Hg}$ concentrations in apex predators quickly, but we also saw a return to pre-manipulation diet and $\mathrm{T}-\mathrm{Hg}$ concentrations 1 year after the experiment. Thus, while managing for prey species with relatively high energy density and low $\mathrm{T}-\mathrm{Hg}$ concentrations represents a potential strategy to reducing $\mathrm{T}-\mathrm{Hg}$ concentrations in predators, sustaining the improved prey base is necessary and may prove unfeasible when prey are maintained through stocking, especially in large systems. Also, in systems where prey fish with relatively high energy density and low $\mathrm{T}-\mathrm{Hg}$ concentrations are already available, adding prey fish with similar characteristics is not likely to reduce predator Hg concentrations. In these situations, predators are likely to already have low Hg concentrations and prey fish subsidies would be unnecessary for the purpose of reducing Hg concentrations of piscivores.

Stocking hatchery fish (particularly large salmonids) as prey for sport fish populations can be expensive, especially at large scales (Johnson and Martinez 2000). In systems where piscivores reproduce naturally, hatchery subsidies have the potential to increase overall predator biomass by contributing to increased growth and reproduction. Thus, stocking can increase consumptive demand of predator populations through time, which may become economically and ecologically unsustainable without the means to control predator abundance (e.g., through liberal harvest or mechanical removal). However, in relatively small systems, or in systems where predator populations are controlled by stocking (i.e., absence of natural reproduction) or intensive harvest, hatchery subsidies offer a means to quickly reduce Hg concentrations in apex predators. When possible, it would be more economically and ecologically feasible to manage for naturally occurring and reproducing populations of prey fish with relatively high energy density and low $\mathrm{T}-\mathrm{Hg}$ concentrations. Similarly, reducing Hg concentrations in apex predators by increasing growth rates through density reduction may also present a more sustainable and cost-effective alternative to stocking prey fish.

Interestingly, despite our initial expectations that smaller northern pike (those with higher growth potential) would preferentially benefit from rainbow trout stocking, larger northern pike gained more mass proportionally relative to smaller northern pike. As a result, larger northern pike (those with the highest initial Hg concentrations) had the highest proportional reduction in Hg concentrations stemming from the experimental manipulation. Though the mechanism for this phenomenon was not evaluated (e.g., differential foraging behavior and (or) success, competitive exclusion, etc.), the implication is that the largest, most contaminated sport fish within a system may experience the largest proportional reductions in Hg concentration from prey stocking. Thus, stocking fewer, larger prey may accomplish similar reductions in Hg concentrations of large sport fish and may focus on the most contaminated individuals in a population, while other, smaller individuals may be more apt to consume other available prey items with relatively low caloric content and high Hg concentrations. It is important to note that we observed differences in the response of northern pike Hg concentrations to the experimental manipulation, and as such, variation in factors at the individual level, including physiology (e.g., elimination rate) and diet composition, must be considered as well as the timing and extent of stocking.

This study used a novel approach, conducting repeated measures of Hg concentrations on individual apex predators at a whole-system scale. To our knowledge, this has not been done in a naturally reproducing sport fish population. Conducting our manipulations at both whole-system and pond scales allowed us to evaluate the variability in responses of apex predators at the individual and population level and at multiple spatial scales. We were able to detect some effects (proportional mass gain as a function of initial northern pike length) at the whole-system scale that we did not observe at the pond scale. Although Hg concentrations of individual northern pike responded to stocking in a similar way at the reservoir and pond scale, the disparate growth responses observed at the reservoir and pond scales highlight the need to conduct studies at the ecosystem scale, when possible, to account for interactions that do not manifest themselves at the microcosm scale. We acknowledge that low sample size in our pond experiment limited our ability to draw inferences. Regardless, the pond and lake results suggest that microcosms alone may not provide reliable insights into responses at larger scales where predator-prey interactions are less constrained. Further, study systems that have been classified as "mesocosms" (e.g., experimental ponds) are still only approximations of natural systems and do not necessarily encompass important processes at work at the whole-system scale (Grice and Reeve 1982; Odum 1984).

Our experimental design allowed us to evaluate the mechanism behind biomass dilution of Hg in predators when growth is increased by the availability of alternate forage over a brief time period. At the temporal scale examined here, it was apparent that the addition of biomass (growth) by predators was the most important factor for reducing Hg concentrations. The maximum rate of Hg dilution in predators in the absence of growth is equivalent to their Hg elimination rate. This will occur when predators consume a maintenance ration of uncontaminated prey. Empirically, we observed rates of Hg dilution in northern pike that exceeded their Hg elimination rate. The bioenergetics simulations indicated that this increased rate was primarily a result of the addition of biomass by northern pike. The simulations also indicated that the rate of predator Hg concentration reduction can be increased to some degree when prey are relatively high in energy density or low in Hg concentration. Thus, in situations arising from changes in food web structure, ontogenetic shifts in diet, or management practices where predator growth rate is increased, prey energy density is increased and (or) prey Hg concentration is decreased, predator Hg concentration can be expected to decrease over time (Sharma et al. 2008; Lepak et al. 2009; Ward et al. 2010), ultimately reaching a new equilibrium if conditions are stable. At the temporal scale of our experiment, the addition of predator biomass was the most important driver of reductions in northern pike Hg concentrations.

This study identified a mechanism that could be artificially depressing Hg levels in aquatic piscivores. Throughout the western United States (and worldwide), millions of rainbow trout are stocked annually as sport fish in put-and-take fisheries and often end up as the primary forage base for apex predators (Marwitz and Hubert 1997; Yule et al. 2000; Flinders and Bonar 2008). Studies have shown that the body condition of top predators is directly related to the stocking of
rainbow trout (McMillan 1984; Marwitz and Hubert 1997; Flinders and Bonar 2008). Additionally, exceptional growth rates of top predators have been related to the availability of soft-rayed prey fishes with high energy density and minimal handling time, such as rainbow trout (Beyerle 1971; Johnson and Martinez 2000). In many western lakes, management strategies reduce predation on rainbow trout by stocking larger fish in favor of fingerlings, which has resulted in increased predation on stocked prey by the largest individuals of the highest trophic position in the system (Wiley et al. 1993; Yule et al. 2000; Flinders and Bonar 2008). This preferential exploitation of stocked subsidies likely is depressing Hg levels in the largest predators of recipient systems, confounding the generally expected trend of increasing body burdens with fish size (and age). This management-induced shift in diet, and associated effects on growth and Hg concentrations, warrants further investigation. Since fish stocking as a management strategy is ubiquitous in fisheries, and our results show that the timing of Hg testing in stocked systems and the extent of stocking events can influence the Hg concentrations in predators, managers and policymakers must consider fish stocking when evaluating sport fish Hg concentrations for the development of consumption advisories in stocked systems.

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## Appendix A

Table A1 on following page.

Table A1. Mercury concentration (wet mass basis) in prey organisms of northern pike sampled from College Lake, the Bellvue-Watson Fish Hatchery, and experimental ponds.

| Species | Length (mm) | Mass (g) | Prep | Site | Analysis | $\begin{aligned} & \mathrm{T}-\mathrm{Hg} / \mathrm{MeHg} \\ & \left(\mathrm{ng} \cdot \mathrm{~g}^{-1}\right) \end{aligned}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| BGL | 79 | 8.1 | MT | Lake | T-Hg | 183.97 |
| CFI | 59 | 4.1 | MT | Lake | MeHg | 21.10 |
| CFI | 75 | 12.5 | MT | Lake | MeHg | 29.50 |
| CFI | 79 | 14.4 | MT | Lake | MeHg | 36.30 |
| CFI | 81 | 16.1 | MT | Lake | MeHg | 32.90 |
| CFI | 85 | 19.7 | MT | Lake | MeHg | 57.60 |
| LMB | 66 | 3.1 | MT | Lake | T-Hg | 113.90 |
| YPE | 76 | 4.0 | MT | Lake | T-Hg | 120.29 |
| YPE | 94 | 9.0 | MT | Lake | T-Hg | 289.39 |
| RBT | 99 | 11.1 | MT | Hatchery | T-Hg | 16.31 |
| RBT | 113 | 16.3 | MT | Hatchery | T-Hg | 23.42 |
| RBT | 116 | 19.8 | MT | Hatchery | T-Hg | 14.44 |
| RBT | 127 | 23.6 | MT | Hatchery | T-Hg | 29.67 |
| RBT | 140 | 28.2 | MT | Hatchery | T-Hg | 21.46 |
| RBT | 150 | 36.3 | MT | Hatchery | T-Hg | 15.07 |
| RBT | 153 | 38.0 | MT | Hatchery | T-Hg | 36.11 |
| RBT | 149 | 39.8 | MT | Hatchery | T-Hg | 15.71 |
| RBT | 157 | 43.1 | MT | Hatchery | T-Hg | 16.95 |
| RBT | 160 | 45.5 | MT | Hatchery | T-Hg | 18.50 |
| RBT | 158 | 46.4 | MT | Hatchery | T-Hg | 20.63 |
| RBT | 158 | 47.2 | MT | Hatchery | T-Hg | 15.43 |
| RBT | 160 | 49.1 | MT | Hatchery | T-Hg | 12.15 |
| RBT | 162 | 53.4 | MT | Hatchery | T-Hg | 17.76 |
| RBT | 197 | 88.0 | MT | Hatchery | T-Hg | 15.93 |
| ANL | 6.5 (HCW) | 0.6 | WB | Ponds | MeHg | 7.67 |
| ANL | 8.0 (HCW) | 1.0 | WB | Ponds | MeHg | 3.98 |
| BGL | 50 | 1.9 | WB | Ponds | T-Hg | 22.29 |
| FMW | 51 | 1.3 | WB | Ponds | T-Hg | 49.33 |
| FMW | 55 | 1.9 | WB | Ponds | T-Hg | 31.97 |
| CHF | 11 (BBL) | 1.3 | MT | Ponds | MeHg | 13.14 |
| CHF | 19 (BBL) | 1.3 | MT | Ponds | MeHg | 17.11 |
| NPK | 19 | 0.1 | WB | Ponds | T-Hg | 62.04 |
| NPK | 25 | 0.1 | WB | Ponds | T-Hg | 34.12 |
| NPK | 38 | 0.3 | WB | Ponds | T-Hg | 39.71 |
| RBT | 109 | 17.5 | MT | Ponds | T-Hg | 23.37 |
| RBT | 130 (BBL) | 75.0 | MT | Ponds | T-Hg | 24.14 |

[^1]
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[^1]:    Note: Species definitions are as follows: ANL, Anisoptera larvae; BGL, bluegill sunfish (Lepomis macrochirus); CFI, crayfish (Orconectes spp.); FMW, fathead minnow (Pimephales promelas); LMB, largemouth bass (Micropterus salmoides); CHF, chorus frog (Pseudacris sp.); NPK, northern pike (Esox lucius); RBT, rainbow trout (Oncorhynchus mykiss); YPE, yellow perch (Perca flavescens). Lengths are as follows: BBL, backbone length (mm); HCW, head capsule width (mm). Types of preparation tissues are as follows: MT, muscle tissue; WB, whole body. Mercury analyses are as follows: MeHg, methylmercury; T-Hg, total mercury. Samples were collected in March from the lake and hatchery and during draining of the experimental ponds.

