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Changes in mercury bioaccumulation in an apex predator in response to removal of an introduced competitor

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Abstract We evaluated methylmercury (MeHg) concentrations in native apex predators, lake trout *Salvelinus namaycush* before and after the large-scale removal of introduced predators, smallmouth bass *Micropterus dolomieu* in a 270 ha Adirondack lake. Previous studies show that removing competitors can result in increased growth and decreased mercury concentrations in remaining fish. Instead, we observed a significant increase in lake trout MeHg concentrations despite observed increases in lake trout growth. Bioenergetics simulations predicted similar increases in lake trout MeHg concentrations. Higher MeHg in prey fish (post-removal diet) relative to invertebrates (pre-removal diet) was the most important factor increasing lake trout MeHg concentrations. However, this effect was counteracted by increased lake trout growth (i.e., growth dilution) likely due to a combination of decreased foraging costs and an increase in prey energy density. These data provide evidence for a mechanism (diet shift due to reduced competition) by which changes in food web structure can influence MeHg concentrations in top predators.

Keywords Mercury · Food web · Fish removal · Growth dilution · Lake trout · Smallmouth bass

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Introduction

Mercury contamination in fish is a serious issue affecting fisheries in the northeastern United States and is of concern worldwide to human and ecosystem health (Bodaly et al. 1993; Johnston et al. 2003; Kamman et al. 2005). The northeastern US receives high levels of atmospheric mercury deposition (Chen et al. 2005; Kamman et al. 2005) and mercury levels in aquatic ecosystems are unlikely to change in the near future (Hunter et al. 2003). Due to bioaccumulation, mercury concentrations are particularly high in large piscivores, i.e., slow-growing fish that feed at the top of aquatic food webs. These large piscivores with high mercury concentrations are frequently targeted for harvest and consumption by anglers.

Methylmercury (MeHg), the primary form of mercury found in sport fish (Bloom 1992), is toxic to humans. An important distinction between MeHg and other forms of mercury is that MeHg is the form that bioaccumulates most readily because it is absorbed by living tissue, therefore MeHg poses a direct threat to humans when it is consumed. It is widely accepted that mercury in sport fish is found primarily (>95%) in the form of MeHg (Bloom 1992), yet total mercury (T-Hg) is often measured as a proxy for MeHg due to higher costs associated with MeHg analyses. Although this assumption holds true for most piscivorous fish, the proportion of MeHg in many organisms consumed by fish (e.g., *Daphnia* sp., chironomids and other invertebrates) is much lower than the generally assumed value (i.e., >95%) for sport fish (Hildebrand et al. 1980; Huckabee et al. 1979; Tremblay and Lucotte 1997). For the remainder of this manuscript we use the following terms: (1) "MeHg" when referring to the methylated form of mercury (2) "T-Hg" when referring to total mercury, and (3) "mercury" when more than one form of mercury is being described.

Mercury bioaccumulation in fish is dependant upon many factors, including fish diet (Harris and Bodaly 1998; Johnston et al. 2003; Swanson et al. 2003), fish trophic position (Power et al. 2002), food web structure (Johnston et al. 2003; Swanson et al. 2003) and energy sources (Power et al. 2002). Previous studies have established that trophic position in predators is positively correlated with increased concentrations of T-Hg (Power et al. 2002). It has also been shown that the mercury content in a predator's diet is the primary source for the mercury accumulated within tissue and that subsequent changes in diet, metabolism, and growth rate can effectively alter mercury concentrations in fish (Harris and Bodaly 1998; MacRury et al. 2002; Trudel and Rasmussen 2006).

The removal of certain fish (predominantly piscivores) from lakes has been proposed as a means to reduce T-Hg concentrations in fish (Göthberg 1983; Rask et al. 1996; Verta 1990). Reductions in fish abundance have been shown to be effective at lowering fish T-Hg concentrations in small lake systems (<25 ha), but the mechanisms behind subsequent decreases in T-Hg accumulation are not well understood (Göthberg 1983; Rask et al. 1996; Verta 1990). Verta (1990) suggested that "growth dilution" was the primary factor leading to decreased T-Hg concentrations in the fish remaining after removal. Growth dilution is a process whereby an increase in fish growth rate leads to lower concentrations of MeHg in fish at a given size or age. For example, growth dilution would occur if the MeHg concentration in a fish's diet remained constant while the energy content of the diet was increased and/or predator growth efficiency was increased. These circumstances could result from an increased abundance of prey items with higher energy density or increased food availability, which could occur in response to a decrease in predator density. The resulting increase in fish growth—without a corresponding increase in prey consumption—would subsequently decrease the overall dietary intake of MeHg per unit of fish tissue growth. Although the outcome of this proposed mechanism would be lower MeHg concentrations in the tissues of faster-growing individuals, this mechanism was not verified in the aforementioned studies (Göthberg 1983; Rask et al. 1996; Verta 1990).

Fish community composition, abundance and food web interactions in aquatic ecosystems are frequently altered by managers of sport fisheries, other anthropogenic impacts, and stochastic natural events (such as fish die-offs). All of these factors have the potential to alter fish density, fish size and age structure, as well as change competitive interactions for resources such as available food and habitat. By quantifying the effects of an intense manipulation—removal of a dominant non-native piscivore—on food web linkages and the bioaccumulation of MeHg in lake trout, we evaluated the influence of changes in food web dynamics on MeHg concentrations in a piscivore population. This large-scale manipulation provided an opportunity to identify factors influencing MeHg concentrations in lake trout, a dominant native predator in north temperate lakes.

Methods

Study site

For five decades, non-native smallmouth bass replaced lake trout as the dominant top predator and reduced native prey fish abundance in the littoral zone of Little Moose Lake, a 270 ha oligotrophic lake in the Adirondack Mountains (New York, USA). An intensive electrofishing effort was initiated in Little Moose Lake in spring 2000 and has continued to the present, resulting in a 90% reduction of adult smallmouth bass abundance with over 60,000 individuals removed to date (Weidel et al. 2007). Prior to smallmouth bass removal, lake trout consumed primarily benthic invertebrates and daphnids (Lepak et al. 2006). The abundance of littoral prey fish increased in response to smallmouth bass removal (Weidel et al. 2007); stable isotope and diet data showed that lake trout began to take advantage of this energy source shortly after removal was initiated (Lepak et al. 2006).

Collections, mercury analysis and statistical comparisons

In order to characterize the effect of smallmouth bass removal on changes in mercury bioaccumulation in lake trout, we evaluated the T-Hg content of fish tissue samples collected and archived from Little Moose Lake from 2000 to 2006. We did not find evidence for growth dilution in our first evaluation of these samples, therefore sought more detail regarding the form of mercury in our fish and invertebrate samples. Thus, lake trout subsequently collected in 2007 were analyzed for T-Hg and MeHg and a correction factor was applied to the empirical measurements of T-Hg in lake trout from previous years (2000–2006) to make comparisons across years. The mean percentage of MeHg relative to T-Hg in the 2007 lake trout was 91.7 ± 2.8% (1 SEM), and this value was used to convert lake trout T-Hg concentrations measured in previous years to MeHg concentrations. Because archived tissue samples were frozen and partially dessicated, results from all fish tissue samples used in this study are reported on a dry weight basis.

Lake trout diet items including prey fish and invertebrates were tested for T-Hg, and a subset of these (collected from lake trout stomachs in 2003–2007) were analyzed for MeHg content. Newly collected and archived

samples of lake trout, prey fish and invertebrates were dried prior to T-Hg and MeHg analyses. For lake trout, only skinless muscle tissue was analyzed. Lake trout diet items were tested for T-Hg by pooling and homogenizing at least 25 individual invertebrate prey items (e.g., chironomids, ephemerids (*Hexagenia*) and daphnids) or two to three fish prey (e.g., rainbow smelt *Osmerus mordax*, smallmouth bass and pumpkinseed sunfish *Lepomis gibbosus*) taken directly from lake trout stomachs. A subsample of the various invertebrate prey items' (chironomids, ephemerids and daphnids) homogenate was also analyzed for MeHg. Additional smallmouth bass ($n = 15$) were analyzed for MeHg as part of another project, and these data were used to allocate the MeHg proportion of T-Hg in smallmouth bass and pumpkinseed sunfish from lake trout diets. No information was available regarding rainbow smelt MeHg concentrations, so we substituted the MeHg proportion of T-Hg for yellow perch *Perca flavescens* from a nearby lake because they have similar feeding patterns as rainbow smelt. We acknowledge the limitations of applying a correction factor to adjust for the proportion of MeHg to T-Hg in lake trout and various prey items, yet the limited availability of temporal, species and system-specific data required this assumption for modeling purposes.

Samples analyzed for T-Hg were prepared by HNO_3 digestion (at 95°C for 3 h in a loosely sealed glass vial) and further oxidation with BrCl prior to analysis. Samples for MeHg and T-Hg analysis were first alkaline digested (at 75°C for 3 h in a sealed glass vial) and an aliquot of the digestate was oxidized with BrCl for analysis of T-Hg. Oxidations using BrCl were performed at 75°C for 30 min under ambient pressure. T-Hg was analyzed by modified EPA 1631, oxidation with $SnCl_2$ reduction, purge, gold trap collection and CVAFS detection. Methylmercury was analyzed using modified EPA 1630, aqueous phase ethylation, purge, Tenax trap collection GC separation and CVAFS detection. Certified reference materials, Dorm-2, IAEA350, IAEA142 and SRM1566b biota tissues were analyzed for quality assessments. Reference samples ($N = 9$) had a mean percent recovery of 95.4%. Duplicate and matrix spike samples were prepared and analyzed for monitoring the precision and accuracy of the analyses. Duplicate samples varied slightly but never more than 4% from the original values with a mean of 1.8 ± 1.8%, and no systematic bias was evident.

Lake trout were collected using a combination of gillnetting, angling and electrofishing in 2000–2007. We focused our field collections and mercury analyses on lake trout approximately 400–500 mm in length in an attempt to standardize for size and because these fish were capable of consuming prey fish, but were not piscivorous prior to the initiation of smallmouth bass removal. Sagittal otoliths were extracted from each lake trout and sagittal sections were prepared and mounted for age interpretation (Secor et al. 1991). A subset (approximately 50) of these otoliths was aged by two readers independently and any discrepancies in age were discussed until the age was agreed upon. The remaining otoliths (approximately 50) were interpreted by a single reader (one of the two mentioned above) with 6 years of experience ageing salmonids using otoliths.

Baseline stable isotope signatures were used to determine lake trout $\delta^{13}C$ and in part trophic position, as described by Lepak et al. (2006). Diet information obtained in 2002 (the most recent substantial collection of lake trout for diet analysis, $N = 93$) were also incorporated to determine lake trout trophic position following Lepak et al. (2006). Additional lake trout diets from fish collected in 2005–2007 were quantified as described in Lepak et al. (2006).

A principal component analysis was conducted to develop a single, multivariate index that could represent changes in lake trout length, weight and age in models accounting for the influence of these factors on key response variables (Niles 1973; Cooch et al. 1999). Due to high correlations between these three size-age metrics, they cannot be used as independent predictors. However, each metric has predictive value and is relatively inexpensive to obtain (when compared to T-Hg or MeHg analyses), therefore all three were included in the principal components analysis. The index developed (referred to as PC1, the size-age principal component) was used to account for differences in length, weight and age by year to evaluate changes in lake trout MeHg concentrations through time. A second principal component incorporating lake trout length, weight and age was developed to explain variation in lake trout MeHg concentration not explained by PC1, but this had little to no additional explanatory value (Pearson correlation coefficient; -0.01, $P = 0.92$) and therefore was not used in further analyses. Changes in lake trout $\delta^{13}C$ and trophic position were also evaluated in models accounting for PC1, year, and relevant interaction terms. A linear regression analysis was conducted to evaluate changes in lake trout growth (as indicated by specific growth rate; % body length/year) over time using age and length data from lake trout collected in 1996 and 1997 (Smith 2000), as well as from lake trout collected in 2000–2002 and 2005–2007, assuming all lake trout began growing at a length of 10 mm (note that only lake trout from 400 to 500 mm in length were used from the 1996 and 1997 collections, adding 76 and 120 lake trout to the data set, respectively). All statistical analyses (principal components analysis, ANCOVA's, Pearson correlations, linear regression analyses and linear trend contrasts) were conducted using SAS (SAS Institute Inc.).

Bioenergetics simulations

Bioenergetics model simulations were implemented to identify potential mechanisms responsible for changes in lake trout MeHg concentration by comparing empirical values of lake trout MeHg with estimated model values. The Wisconsin Fish Bioenergetics Model 3.0 (Hanson et al. 1997; applying default lake trout parameters, Stewart et al. 1983) was used to estimate individual lake trout MeHg concentration using two scenarios based on observed lake trout diet and growth prior to and following the smallmouth bass removal. We specifically evaluated the relative influence of lake trout prey energy density, lake trout growth efficiency and lake trout prey MeHg concentration upon lake trout MeHg concentration by comparing pre and post-removal conditions associated with the smallmouth bass manipulation (Lepak et al. 2006; Weidel et al. 2007). We also varied MeHg concentrations and energy content of prey items ±10% under both scenarios to evaluate the influence of these factors on lake trout MeHg concentrations.

The pre-removal simulation was designed to mimic the growth of an individual lake trout prior to the initiation of the smallmouth bass removal using the mean age (12.5 years) of 15 lake trout collected in 2000 that grew to a mean weight of 761 g. Although diets from only 15 lake trout were available from 2000, the diet composition of these fish was similar to that of fish collected in 1996 and 1997 ($N = 99$, collected May–September and $N = 89$, collected from January to October, respectively). Similar proportional masses of the top three diet items; chironomids, ephemerids (primarily *Hexagenia*) and daphnids (see Lepak et al. 2006) were found in fish collected in 1996, 1997, and 2000, therefore diets from 2000 were used in pre-removal simulations.

The post-removal simulation used the maximum annual lake trout growth rate observed following the smallmouth bass removal to evaluate the maximum potential impact of growth dilution on an individual lake trout's MeHg concentration. The maximum mean growth rate was observed in fish collected in 2006 with a mean age of 7.5 years and corresponding mean weight of 745 g. Diets from lake trout collected in 2002 (primarily consisting of rainbow smelt, smallmouth bass and pumpkinseed sunfish) were used for the post-removal diets in the simulations because of the relatively large sample size and seasonal breadth.

The most common three diet items in lake trout stomachs (accounting for >70% of lake trout diet dry weight) were set to comprise 100% of the diets for the purposes of the simulations under both pre- and post-removal conditions (Table 1). The remaining diet items were diverse (e.g., corn kernels, stones, fish eggs, frogs, leeches, vegetation etc.,) and contributed relatively little to lake trout diets by weight, plus little to no information was available regarding their MeHg concentrations. Estimates of energy densities for diet items were compiled from the literature (Cummins and Wuycheck 1971; Hanson et al. 1997; Rand et al. 1994).

Table 1 Taxonomic composition, energy density and mercury content of lake trout diets before and after the implementation of the smallmouth bass removal in Little Moose Lake

	Proportion (%)	Energy (J/g)	Mercury (μg/g)	% Methyl
Pre-removal diet				
Chironomids	63	2,747	0.023	31
Hexagenia	34	4,706	0.040	36
Daphnia	3	2,514	0.036	25
Post-removal diet				
Rainbow smelt	43	4,865	0.030	100
Smallmouth bass	39	4,186	0.030	81
Pumpkinseed sunfish	18	4,186	0.038	81

The three most abundant diet items were set to represent 100% of lake trout diets. Estimates of energy densities, total mercury (mg/Kg) and percentage of total mercury that was in the methylated form are shown

Bioenergetics simulations were used to estimate the mass of the consumed diet items required for an individual lake trout to achieve the growth observed under pre- and post-removal conditions. These values were estimated daily and were then used to estimate the MeHg concentration in a lake trout using the following equation:

$$\mathrm{MeHg_{LT}} = \sum \left[\left(\alpha \times C \times \mathrm{MeHg_{prey}} \right) - E \right] / W \qquad (1)$$

where $\mathrm{MeHg_{LT}}$ is lake trout MeHg concentration (μg/g), α is the assimilation efficiency of MeHg, C is daily consumption in grams, $\mathrm{MeHg_{prey}}$ is the lake trout prey items MeHg concentration (μg/g), E is the MeHg elimination rate (μg/day) and W is the estimated lake trout weight in grams. These simulations were carried out for 12.5 and 7.5 years for the pre and post-removal conditions, respectively. The cumulative numerator divided by daily lake trout weight in Eq. 1 provides estimates of lake trout MeHg concentrations through time. The assimilation efficiency of MeHg was assumed to be 0.8, reflecting the assimilation efficiency of sulfur-containing proteins to which MeHg is covalently bound (Brett and Groves 1979; Harris et al. 2003; Trudel and Rasmussen 2006). The elimination rate (E) of MeHg was calculated using the following equation developed by Trudel and Rasmussen (2001):

$$\mathrm{Ln}(E) = 0.066(T) - 0.2 \times \mathrm{Ln}(W) - 5.83 \qquad (2)$$

where E is the elimination rate of MeHg (μg/day), T is the water temperature (°C) and W is the weight of the fish in grams. Water temperatures to which fish were exposed

were estimated using data obtained from a temperature logger placed at a depth of 10 m in Little Moose Lake in 2004 and 2005.

We assumed that lake trout were not sexually mature for the purposes of the simulation (maturation ranges from approximately 7 to 11 years of age in this population, J. Robinson and N. Smith, unpublished data) and other investigators have observed that elimination of T-Hg from eggs and sperm is negligible in lake trout relative to other losses (Trudel and Rasmussen 2001). The bioenergetics simulations also assumed that the majority of MeHg in lake trout tissue came from dietary sources and not from exchange with the water column (Harris and Bodaly 1998; Johnston et al. 2003).

Results

Empirical findings

Lake trout collected from 2000 to 2007 were between 362 and 551 mm in length with a mean length of 456 ± 3 mm (1 SEM). Shortly after the initiation of the smallmouth bass removal (2002–2007) diets of these predators were dominated by fish prey (>70% by dry weight). Based on the diet data available from 15 lake trout collected each year from 2005 to 2007, lake trout primarily consumed smallmouth bass, followed (in order of respective abundance) by small lake trout, rainbow smelt, slimy sculpin *Cottus cognatus* and pumpkinseed sunfish, though we caution that these data were limited in number and seasonal scope.

No trend was observed over time in the first principal component (PC1) encompassing lake trout size and age (e.g., length, weight and age) (ANCOVA; $F_1 = 0.41$, $P = 0.52$, coefficient $= -0.04$). A model developed to evaluate the importance of year and the lake trout size-age principal component upon lake trout MeHg (MeHg = year + PC1 + year × PC1) indicated that PC1 was the most important factor associated with lake trout MeHg (ANCOVA; $F_1 = 25.13$, $P < 0.01$, coefficient $= 0.06$) followed by year (ANCOVA; $F_5 = 3.19$, $P = 0.01$, coefficient $= 0.07$) and the interaction term, which was not statistically significant and was excluded from further analyses (ANCOVA; $F_5 = 1.99$, $P = 0.09$). Overall, PC1 accounted for a significant amount of variation in lake trout MeHg concentrations ($R^2 = 0.22$). A linear trend contrast showed that from 2000 to 2007 lake trout MeHg concentrations increased significantly ($F_5 = 7.58$, $P < 0.01$; see Fig. 1).

A model developed to evaluate the influence of year and PC1 upon lake trout δ^{13}C (δ^{13}C = year + PC1 + year × PC1) indicated that the size-age principal component was the most important factor for predicting lake trout δ^{13}C (ANCOVA; $F_1 = 7.80$, $P < 0.01$, coefficient $= 0.34$) followed by year (ANCOVA; $F_5 = 3.07$, $P = 0.01$, coefficient $= 0.24$) and the interaction term, which was not statistically significant and was excluded from further analyses (ANCOVA; $F_5 = 1.60$, $P = 0.17$). A linear trend contrast showed that from 2000 to 2007, lake trout δ^{13}C increased significantly ($F_1 = 8.23$, $P < 0.01$; see Fig. 2).

A model developed to evaluate the importance of year and PC1 for predicting lake trout trophic position (trophic position = year + PC1 + year × PC1) showed that year was the most important factor (ANCOVA; $F_5 = 4.87$, $P < 0.01$, coefficient $= 0.02$) followed by PC1 (ANCOVA; $F_1 = 4.38$, $P = 0.04$, coefficient $= 0.01$) and the interaction term, which was not statistically significant and was excluded from further analyses (ANCOVA; $F_5 = 1.87$, $P = 0.11$). A linear trend contrast showed that from 2000 to 2007, lake trout trophic position has not increased significantly ($F_1 = 0.01$, $P = 0.91$; see Fig. 3). Earlier findings showed an initial increase in lake trout

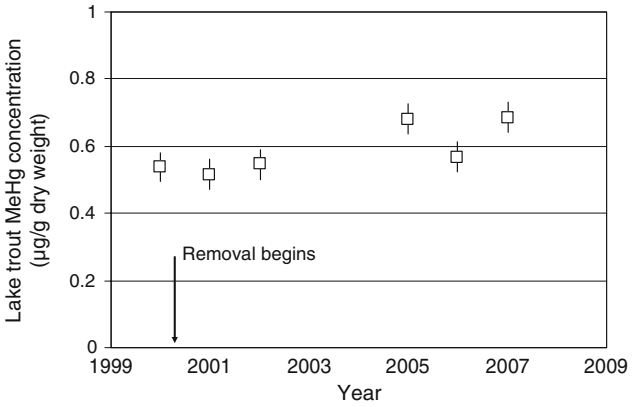

Fig. 1 The annual least squares mean value for lake trout MeHg (µg/g) is presented for each sampling year as a proportion of dry weight, while taking into account the influence of PC1. $N = 15$ for all points; *error bars* represent one SEM

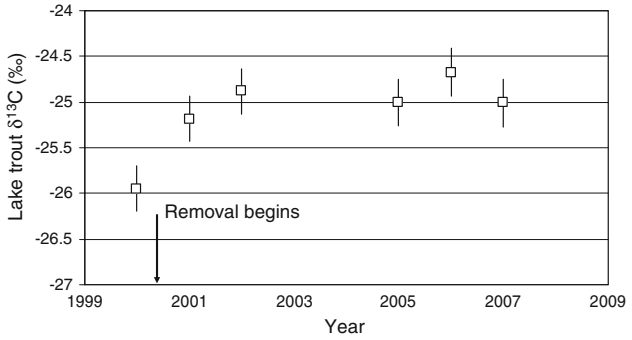

Fig. 2 The annual least squares mean value of lake trout δ^{13}C (‰) is presented for each sampling year, while taking into account the influence of PC1. $N = 15$ for all points; *error bars* represent one SEM

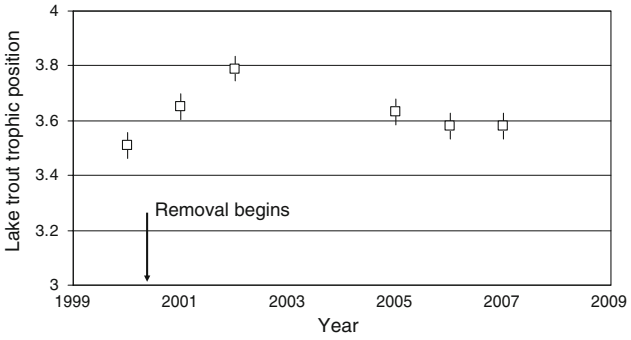

Fig. 3 The annual least squares mean value for lake trout trophic position is presented for each sampling year, while taking into account the influence of PC1. $N = 15$ for all points; *error bars* represent one SEM

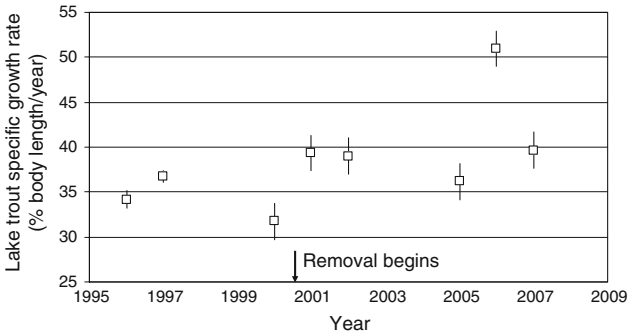

Fig. 4 The mean annual lake trout specific growth rate (% body length/year) is presented for each sampling year. Note; only lake trout between 400 and 500 mm captured in 1996 and 1997 were included in this analysis, adding 76 and 120 fish to this analysis, respectively. $N = 15$ for all points from 2000 and later; *error bars* represent one SEM

trophic position (Lepak et al. 2006), but this trend has not continued through time.

Lake trout δ^{13}C and trophic position were correlated (Pearson correlation coefficient; 0.42, $P < 0.01$). Because we were interested in the importance of diet source and trophic position relative to changes in lake trout MeHg concentration, the effects of δ^{13}C and trophic position were evaluated individually. Individual models were developed for δ^{13}C and trophic position (MeHg = δ^{13}C + year + PC1 and MeHg = trophic position + year + PC1, respectively). Neither lake trout δ^{13}C nor trophic position effectively explained the observed variation in lake trout MeHg (ANCOVAs; $F_{1,1} = 0.21$ and 1.59, $P = 0.65$ and 0.21, coefficients = 0.01 and 0.13, respectively). Trophic position explained more of the variability in lake trout MeHg concentration than δ^{13}C, but this relationship was not significant. More detailed scatter plots of the relationships between lake trout MeHg concentrations by year and PC1, δ^{13}C and trophic position are provided in Appendix 1. Pearson correlation coefficients and significance of relationships between all of the parameters described above (MeHg, PC1, Year, δ^{13}C and trophic position) are provided in Appendix 2.

Lake trout growth increased significantly from 1996 to 2007 (Fig. 4). Combining data from 1996 to 1997, 2000 to 2002 and 2005 to 2007, a linear regression analysis revealed a significant increase in lake trout specific growth rate interpreted from otoliths ($F_7 = 9.87$, $P < 0.01$, coefficient = 0.68; Note that only lake trout from 400 to 500 mm in length were used from the 1996 and 1997 collections, adding 76 and 120 lake trout to the data set, respectively).

Bioenergetics simulation findings

Simulation results indicated that altering the MeHg concentrations and energy content of lake trout diet items resulted in changes in lake trout MeHg concentration (Table 2). Increasing energy density in lake trout prey items (leading to higher growth efficiency of lake trout) in the simulations resulted in decreases in lake trout MeHg concentrations that were of similar magnitude to those associated with MeHg increases caused by increasing MeHg concentrations in lake trout prey items (Table 3). However, the estimates of MeHg concentration in lake trout prey items was almost threefold higher in prey fish (post-removal diet) relative to invertebrates (pre-removal diet) while energy densities of prey items increased only an estimated 24% from the pre-removal to post-removal periods (Table 2).

The bioenergetics simulations showed that although lake trout were growing faster following the smallmouth bass removal, they were still expected to have higher MeHg concentrations relative to the period before the removal, and this prediction agrees with our empirical observations. The pre- and post-removal bioenergetics simulations estimated lake trout MeHg concentrations of 0.58 μg/g dry weight and 0.87 μg/g dry weight, respectively, while the MeHg concentrations of lake trout sampled from Little Moose Lake before and after the removal were approximately 0.5 μg/g dry weight and 0.7 μg/g dry weight, respectively. Mean estimated lake trout consumption rates (% body weight/day) were 1.6 ± 0.7 (1 SD) for the pre-removal simulation and 1.4 ± 0.8 (1 SD) for the post-removal simulation. Estimated daily lake trout consumption rates were consistently higher (mean difference of 0.54 ± 0.17, 1 SD) under the pre-removal simulation conditions relative to the post-removal simulation conditions. Mean estimated lake trout growth rates (% body weight/day) were 0.10 ± 0.11 (1 SD) for the pre-removal simulation and

Table 2 Estimates of the energy content and MeHg concentration of the composite lake trout diet and lake trout growth efficiency before and after the implementation of the smallmouth bass removal in Little Moose Lake

	Pre-removal	Post-removal	Proportional change (%)	Effect on lake trout MeHg
Energy content of diet (J/g wet)	3,406	4,478	24	MeHg down
Growth efficiency (%)	5%	10%	100	MeHg down
MeHg of diet (μg/g)	0.010	0.028	280	MeHg up

The proportional change in each, and the corresponding post-removal effect on lake trout MeHg concentration is also shown

Table 3 Influence of proportional changes in lake trout prey energy content and MeHg concentration relative to baseline bioenergetics simulations for pre and post-removal conditions

	Age (years)	Growth (g)	Total consumption (g)	Growth efficiency (%)	Total MeHg (μg)	MeHg by dry weight (μg MeHg/g)	Change (%) from baseline
Pre-removal							
Energy content (−10%)	0–12.5	751	15,757	4.8	121.8	0.65	12.0 (+)
MeHg (+10%)	0–12.5	751	14,073	5.3	119.6	0.64	10.0 (+)
Baseline	0–12.5	751	14,073	5.3	108.7	0.58	0.0
MeHg (−10%)	0–12.5	751	14,073	5.3	97.9	0.52	10.0 (−)
Energy content (+10%)	0–12.5	751	12,719	5.9	98.3	0.52	9.7 (−)
Post-removal							
Energy content (−10%)	0–7.5	735	8,038	9.1	179.4	0.98	13.6 (+)
MeHg (+10%)	0–7.5	735	7,192	10.2	176.7	0.96	10.0 (+)
Baseline	0–7.5	735	7,192	10.2	160.5	0.87	0.0
MeHg (−10%)	0–7.5	735	7,192	10.2	144.5	0.79	10.0 (−)
Energy content (+10%)	0–7.5	735	6,508	11.3	145.3	0.79	9.6 (−)

Growth efficiency is represented by growth divided by total consumption. Total exposure of lake trout to MeHg from prey is shown (Total MeHg) and the resulting lake trout MeHg concentration based on bioenergetics simulations is shown. The percent change in lake trout MeHg concentration resulting from varying lake trout prey energy content and MeHg concentration is shown as a difference from the respective baseline estimation for pre- and post-removal simulations. The initial lake trout weight was 10 g in all cases. Pre-removal conditions simulated fish growth to 761 g while post-removal conditions simulated fish growth to 745 g

0.16 ± 0.13 (1 SD) for the post-removal simulation. Estimated daily lake trout growth rates were consistently lower (mean difference of 0.03 ± 0.03, 1 SD) under pre-removal simulation conditions relative to the post-removal simulation conditions.

Discussion

Given previous observations of T-Hg growth dilution in empirical studies and corroborative model predictions (Borgmann and Whittle 1992; Göthberg 1983; Rask et al. 1996; Simoneau et al. 2005; Verta 1990), our observations of increased growth and increasing MeHg concentrations in lake trout were surprising. We expected that the increased lake trout growth observed following the smallmouth bass removal would result in lower MeHg concentrations. Instead, we observed changes in fish diets that increased lake trout MeHg concentrations because lake trout began consuming prey fish that had much higher concentrations of MeHg relative to invertebrate prey that previously dominated their diets. This increase occurred despite lake trout post-removal diets being higher in energy content and the likely decrease in lake trout foraging activity resulting from the smallmouth bass manipulation. These conditions resulted in higher lake trout growth efficiency and estimated lower overall consumption (as supported by the bioenergetics simulations) of contaminated prey relative to pre-removal conditions; however, the empirical and model results show that this mechanism was overwhelmed by a large increase in lake trout diet MeHg concentrations.

The lake trout size-age principal component (PC1) and sampling period were better estimators of lake trout MeHg concentration than isotopic metrics of energy source and trophic position. This suggests that lake trout size-age and time of collection relative to the initiation of the

smallmouth bass removal were the most important predictors of lake trout MeHg concentrations within the study lake. In accord with previous observations based on 3 years of data (2000–2002; Lepak et al. 2006), lake trout from Little Moose Lake continued to consume prey fish and obtained energy from littoral energy sources in subsequent years (2005–2007), as was reflected by lake trout $\delta^{13}C$ signatures. However, the trophic position of lake trout appears to have declined slightly since 2002, despite the initial increase in lake trout trophic position observed in following initiation of the smallmouth bass removal (Lepak et al. 2006). It is possible that littoral prey fish in Little Moose Lake are now lower in trophic position and/or smaller in size due to increased competition for food, given that the relative abundance of prey fish has increased substantially in response to the bass removal (Weidel et al. 2007). These changes in lake trout trophic position suggest that food web changes are continuing to occur in response to the large-scale removal of a non-native dominant predator, but the mechanism behind these observations has not been identified. We will therefore continue to monitor the lake trout population as this food web is exposed to post-removal conditions for longer periods of time.

Varying the energy content of lake trout diets in the bioenergetics simulations demonstrated that growth dilution can be an important factor in determining MeHg concentrations in fish. However, the estimated increases in lake trout MeHg concentrations were not as high as what would have been expected based on estimated changes in lake trout prey energy density (and subsequently growth efficiency) and MeHg concentrations alone. This indicates that although prey energy density may be an important factor producing growth dilution in lake trout, other factors not evaluated here (e.g., lake trout activity) may be influencing lake trout MeHg bioaccumulation as well. Additionally, the bioenergetics estimates in this study, based on post-removal conditions, overestimated lake trout MeHg concentrations (0.87 μg/g dry weight) relative to the empirical mean value (0.65 μg/g dry weight) measured during the post-removal period. Although activity was not evaluated in this study, this discrepancy observed between empirical and estimated lake trout MeHg concentrations could be attributed to a decrease in lake trout foraging activity under post-removal conditions.

Previous studies have shown that T-Hg concentrations in lake trout are positively correlated with activity (Trudel and Rasmussen 2001, 2006). Similarly, Rennie et al. (2005) used a contaminant model and two other independent measures to demonstrate that a slow-growing yellow perch population was approximately 30% more active and twice as contaminated with MeHg relative to a fast-growing yellow perch population found in a similar system. Both populations were feeding on benthic invertebrates with similar MeHg concentrations, and no significant differences in prey availability were found. We observed increases in littoral prey fish abundance and consumption by lake trout within our study lake, indicating that these prey are now more readily available to predatory fish. We expect that the activity costs of lake trout feeding on prey fish are lower than for lake trout feeding on invertebrates because a single prey fish provides the same amount of energy as gained by consuming hundreds or more individual invertebrate prey items. This is supported by the observations of Pazzia et al. (2002) who found that piscivorous lake trout grew more efficiently than lake trout consuming invertebrates and that greater activity costs for non-piscivorous lake trout foraging on small prey items accounted for this difference.

We were unable to evaluate differences in lake trout activity in Little Moose Lake before and after the smallmouth bass manipulation due to the difficulty of quantifying fish activity in field studies. However, the simulation results presented here suggest that a combination of increased prey energy density and decreased foraging activity compensated for a reduction in food intake—thereby leading to an increase in lake trout growth following the smallmouth bass removal. Other investigators have assumed that lake trout consumption rates are positively correlated with foraging activity (Trudel and Rasmussen 2006). Estimated mean consumption rates of the slower-growing lake trout (pre-removal simulation) in this study were approximately 1.4 fold greater than those of faster-growing fish (post-removal simulation), suggesting activity was higher for lake trout consuming invertebrates. Trudel and Rasmussen (2006) described changes in lake trout MeHg biomagnification factor (BMF; a dimensionless metric indicating the ratio of MeHg concentration in fish to the MeHg concentration in their food) in terms of the activity multiplier (ACT; a dimensionless metric representing activity costs), consumption rates, growth rates and gross growth efficiency. Over the ranges of consumption, growth and growth efficiency estimated in our bioenergetics simulations, a decrease in lake trout ACT from 2 to 1 would produce a decrease in lake trout BMF that would account for the discrepancy between our simulated post-removal lake trout MeHg estimates and empirical values.

We note that bioenergetics simulations in our study were sensitive to changes in prey MeHg concentrations, which is particularly important given that MeHg concentrations in invertebrates and fish have been shown to vary significantly (Ward and Neumann 1999; Suchanek et al. 2008). If variation in lake trout prey MeHg concentrations occur within the study system, inaccurate characterization of prey MeHg concentrations could also account for discrepancies between our empirical and simulation findings. As such, we

caution against over-interpretation of simulation results given the lack of comprehensive data for lake trout prey MeHg concentrations and measures of lake trout activity before and after the smallmouth bass manipulation. Thus, the degree to which differences in prey energy density and activity were responsible for growth dilution in the lake trout population in Little Moose Lake is unknown, but our findings suggest that large increases in prey MeHg concentration (resulting in an overall increase in lake trout MeHg concentration) were offset in some part by increases in prey energy density and to some extent by a reduction in lake trout foraging activity, leading to increased growth efficiency.

The results from this study suggest that changes in food web structure and dynamics can have a large influence on MeHg concentrations in top predators such as lake trout. Specifically, alterations in fish density can influence MeHg concentrations in individuals remaining within a lake system. This mechanism could potentially be used to increase fish growth rates while maintaining or reducing levels of T-Hg intake, resulting in growth dilution as has been observed previously (Göthberg 1983; Rask et al. 1996; Verta 1990). But more importantly, several food web components and other important factors must be characterized before changes in MeHg concentrations in fish can be understood in response to changes in fish community composition. For example, this research, Pazzia et al. (2002) and Trudel and Rasmussen (2006) have shown that field assessments of lake trout activity costs would contribute greatly to the understanding of MeHg bioaccumulation. Also, it is important to consider prey MeHg concentrations when using bioenergetics simulations to investigate MeHg bioaccumulation in top predators. Thus, it is necessary to understand the food web dynamics of a particular system (e.g., foraging behavior, the energy and MeHg content of prey resources, fish growth) in order to determine how alterations in lake food webs influence the MeHg concentrations in sport fish.

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Appendix 1

See Fig. 5.

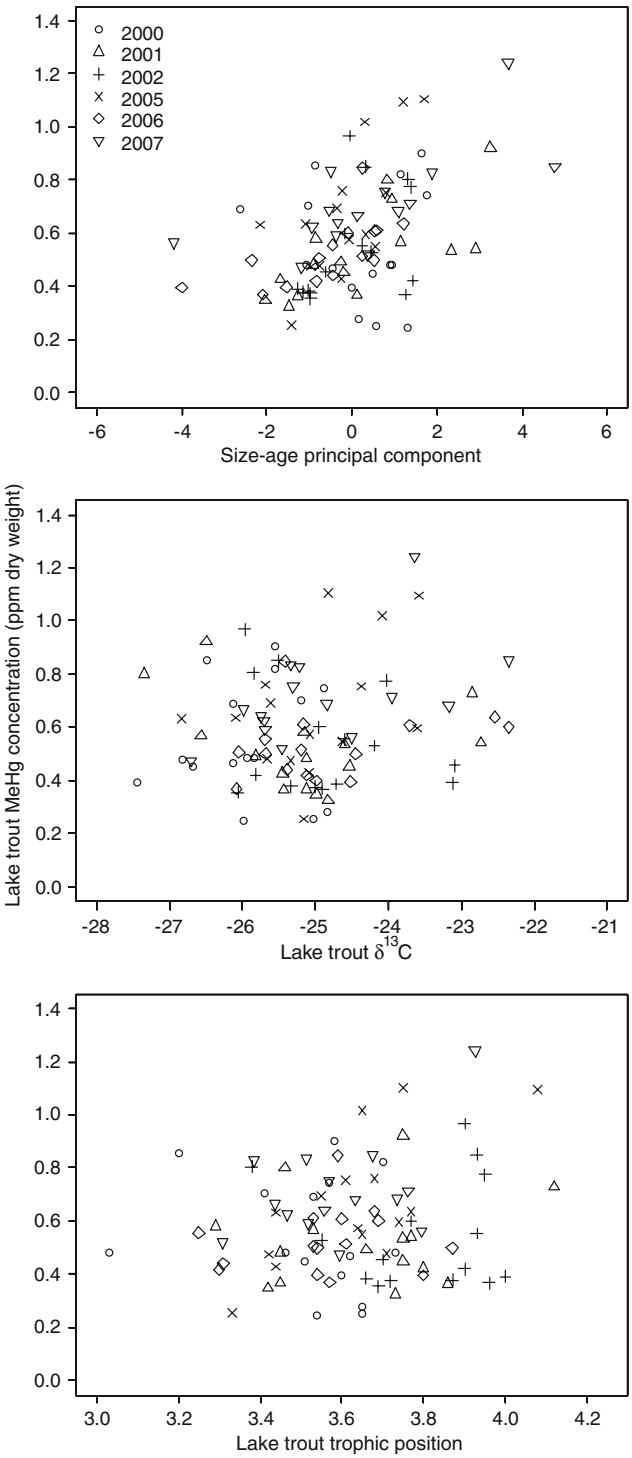

Fig. 5 Scatter plots of lake trout MeHg concentrations by year as a function of lake trout size-age principal component, $\delta^{13}C$ and trophic position

Appendix 2

See Table 4.

Table 4 Pearson correlation coefficients and significance of the relationships between lake trout MeHg concentrations, PC1, year, lake trout $\delta^{13}C$ and trophic position

	PC1	Year	$\delta^{13}C$	Trophic position
MeHg	0.47 (<0.01)	0.23 (0.03)	0.14 (0.20)	0.15 (0.15)
PC1		−0.07 (0.52)	0.28 (<0.01)	0.17 (0.13)
Year			0.24 (0.02)	−0.07 (0.51)
$\delta^{13}C$				0.42 (<0.01)

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