

Rapid food web recovery in response to removal of an introduced apex predator

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Abstract: Non-native species have increased extinction rates, decreased diversity, altered organism distributions, and constrained ecosystem functioning in native aquatic and terrestrial communities. Although widespread fish introductions have dramatically altered fish communities in north temperate lakes, restoration of native fish communities has been rarely accomplished. This study evaluated a native fish community restoration using a stable isotope based metric. Stable isotopes from a native apex predator (lake trout (*Salvelinus namaycush*)) were used to measure food web changes following removal of a dominant non-native apex predator (smallmouth bass (*Micropterus dolomieu*)). Prior to bass removal, lake trout consumed primarily invertebrates. Within 2 years of the initiation of an experimental removal effort, lake trout $\delta^{13}\text{C}$ values (-25.9‰ to -24.9‰) and trophic position (3.5–3.9) increased, reflecting a switch to prey fish consumption that was supported by stomach contents analyses. Here, we show the rapid reestablishment of food web linkages within a native fish community in response to changes in principal energy sources and trophic position of a native apex predator along with the ability to quantify the extent of these changes.

Résumé : Les espèces non indigènes accroissent les taux d'extinction, réduisent la diversité, modifient la répartition des organismes et gênent le fonctionnement des écosystèmes des communautés indigènes aquatiques et terrestres. Bien que les introductions répandues de poissons aient modifié de façon très sérieuse les communautés de poissons des lacs nordiques tempérés, on a rarement réussi à rétablir les peuplements indigènes de poissons. Notre étude évalue la restauration d'un peuplement indigène de poissons à l'aide d'une métrique basée sur les isotopes stables. Les isotopes stables d'un prédateur du sommet du réseau alimentaire (le touladi, *Salvelinus namaycush*) nous servent à mesurer les changements dans le réseau après l'élimination d'un prédateur supérieur dominant non indigène (l'achigan à petite bouche, *Micropterus dolomieu*). Avant le retrait des achigans, les touladis consommaient surtout des invertébrés. En moins de deux ans après le début de l'expérience de retrait expérimental, il y a eu une augmentation des valeurs de $\delta^{13}\text{C}$ ($-25,9\text{‰}$ à $-24,9\text{‰}$) et de la position trophique (3,5–3,9) chez le touladi qui reflète un passage à la consommation de poissons comme proies, ce qui est confirmé par les analyses des contenus stomacaux. Nous montrons ici un rétablissement rapide des liens du réseau alimentaire dans un peuplement de poissons indigènes en réaction à des changements des principales sources d'énergie et de la position trophique d'un prédateur supérieur indigène. Nous avons aussi pu évaluer quantitativement l'importance de ces changements.

[Traduit par la Rédaction]

Introduction

Anthropogenic impacts upon north temperate lake ecosystems include broad alterations to lake chemistry (Carpenter et al. 1998; Stoddard et al. 1999) and biotic communities (Whittier and Kincaid 1999). Although methods are available to evaluate water quality restoration within lakes, easily interpretable metrics related to complex energy dynamics have not been used for evaluating restoration of fish communities. Stable isotope analyses have been suggested as a metric to assess fish communities and evaluate the energy dynamics across trophic levels (Vander Zanden et al. 1999, 2003). While stable isotopes have demonstrated the long-term negative impacts of introduced species and the loss of trophic position, no study has yet demonstrated that stable isotopes can also rapidly and effectively document fish com-

munity restoration. We implemented a lake manipulation experiment removing a dominant non-native apex predator to test the hypothesis that stable isotope measurements could be used to quantify the restoration of lake food web linkages following reestablishment of a native fish community.

Non-native fishes have decimated native fish communities and reduced the trophic position of native apex fish predators in north temperate lakes (Vander Zanden et al. 1999; Whittier and Kincaid 1999; Jackson 2003). Specifically, smallmouth bass (*Micropterus dolomieu*) are recognized as a primary threat to native fish communities throughout the eastern United States and Canada because they reduce littoral fish abundance and disrupt food web linkages (Chapleau and Findlay 1997; Findlay et al. 2000). Vander Zanden et al. (1999) used stable isotope analyses to demonstrate that bass were capable of displacing native lake trout (*Salvelinus*

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namaycush) as apex predators in a set of lake systems by altering food webs, thereby shortening the food chain length and decreasing mean lake trout trophic position. $\delta^{13}\text{C}$ values presented by Vander Zanden et al. (1999) showed that lake trout in lakes where bass were absent were enriched relative to those that had been invaded by bass, indicating a decrease in the amount of littoral prey fish in lake trout diets.

For five decades, non-native smallmouth bass have replaced lake trout as the dominant apex predator and reduced native prey fish abundance in the littoral zone of our study lake, a 271 ha oligotrophic lake (Little Moose Lake, Herkimer County, New York) (Brown et al. 2000; Weidel et al. 2000). Throughout this period of bass dominance, the lake trout population within Little Moose Lake consisted largely of nonpiscivorous lake trout that grew slowly and matured at small sizes (Smith 2000), similar to populations in Ontario lakes described by Martin (1966) and Konkle and Sprules (1986).

An intensive electrofishing effort was initiated and maintained in Little Moose Lake from spring 2000 through fall 2002, resulting in a 90% reduction of adult smallmouth bass (more than 28 000 individuals were removed). Prey fish catch per unit effort increased in spring electrofishing surveys from 2000 to 2002 (greater than twofold increases in abundance were observed for common prey fishes such as brown bullhead (*Ameiurus nebulosus*), pumpkinseed (*Lepomis gibbosus*), and slimy sculpin (*Cottus cognatus*), all of which are consumed by lake trout) (Weidel 2004). Based on these changes in littoral prey fish abundance, we hypothesized a shift in lake trout $\delta^{13}\text{C}$ signatures from values indicative of pelagic–profundal energy sources to more littoral values, and we expected lake trout trophic position, as measured by $\delta^{15}\text{N}$, to increase owing to increased fish consumption (Vander Zanden and Rasmussen 1999; Post 2002).

Materials and methods

Stable isotope baseline characterization

Following methods in Post (2002), littoral, pelagic, and profundal baselines for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in Little Moose Lake were established by analyzing a wide range of invertebrates (Diptera, Odonata, Ephemeroptera, Trichoptera, Gastropoda, and Cladocera) and algae collected from May through August 2000–2002. For organisms with a second-order trophic position (i.e., consumers of primary producers), 3.4‰ was subtracted from their measured $\delta^{15}\text{N}$ signature to establish a baseline $\delta^{15}\text{N}$ value for trophic level 1.

To ensure that sample storage did not influence stable isotope measures, all tested organisms were collected while still alive and then preserved and processed such that fractionation or decomposition did not occur (Post 2002). Two to 50 organisms collected on a given sampling date were homogenized and assayed whenever a single organism did not provide enough material (0.9 mg) for stable isotope analysis. Stable isotopes in prey fish (ranging from 40 to 150 mm and considered consumable by lake trout ranging in length from 264 to 551 mm) were also measured to establish a lake trout isotopic signature that would be expected if they maintained a strictly piscivorous diet.

Lake trout collections and processing

Diet contents were collected and stable isotopes values were measured from 159 lake trout (264–551 mm) collected from April 2000, 1 month prior to initiation of bass removal, through June 2002 by electrofishing, trap netting, and angling.

Gastric lavage was used to collect stomach contents. The procedure was carried out by inserting a soft flexible tube into a lake trout's esophagus and then pumping distilled water into the stomach to expel the contents. This procedure was repeated at least twice for every fish. Lake trout that were thought to still contain stomach contents after manual and visual evaluation were subjected to a third gastric lavage procedure. The effectiveness of this method was evaluated by dissecting approximately 20 fish. In over 90% of these cases, 90% of available stomach contents (by wet weight) were successfully retrieved from the subject fish and minimal residue remained in the stomach.

Lake trout tissue samples were collected from the anterior–dorsal musculature with a biopsy procedure using a 14-gauge, 6 cm needle. Lipids were extracted from all lake trout tissue before analysis (see methods in Folch et al. 1957; Post and Parkinson 2001) to account for the differential routing of stable isotopes in adipose versus muscle tissue (DeNiro and Epstein 1978; Peterson and Fry 1987; Kling et al. 1992).

Littoral carbon estimation

Proportions of littoral and pelagic–profundal energy contributions to lake trout tissue were estimated by comparing $\delta^{13}\text{C}$ measurements of lake trout muscle with invertebrate samples. Equation 1 (following Vander Zanden et al. 1999) was used to estimate the relative contribution of littoral energy to lake trout tissue samples, assuming that energy sources were either littoral or pelagic–profundal:

$$(1) \quad \% \text{ littoral} = \frac{(\delta^{13}\text{C}_{\text{lake trout}} - \delta^{13}\text{C}_{\text{pelagic-profundal}})}{(\delta^{13}\text{C}_{\text{littoral}} - \delta^{13}\text{C}_{\text{pelagic-profundal}})} \times 100$$

Diet analysis

Stomach contents were identified and categorized as littoral, pelagic, or profundal as well as fish or non-fish. Stable isotope signatures, life history traits, known distributions, and behavior of organisms were all taken into account when assigning organisms to a lake region (e.g., littoral, pelagic, or profundal). Diet item dry weights were calculated using intact organisms collected from Little Moose Lake of comparable size with those found in lake trout stomachs. Dry weight was estimated by drying organisms for 24–72 h at 60 °C depending on their size.

Lake trout diet data were pooled from every fish sampled in a given year to represent the overall diets throughout the year. These annual diet compilations were used to calculate the relative contribution of littoral, pelagic, and profundal energy sources from 2000 to 2002. Comparison of our results with lake trout dietary data collected from Little Moose Lake during 1996–1997 confirmed that seasonal variation did not greatly influence stomach contents. The 1996 and 1997 diet data encompassed a wider seasonal range (March–December and January–October, respectively) than the

2000–2002 diet data (April–September, May–December, and January–August, respectively).

Trophic position quantification

A three-source-mixing model, incorporating lake trout diet data, was developed to quantify lake trout trophic position (eq. 2) where TP_{It} represents lake trout trophic position; α , β , and γ ($\alpha + \beta + \gamma = 1$) represent the proportion of lake trout diets composed of littoral, pelagic, and profundal energy sources, respectively, based on annual stomach content data; and λ is the trophic position of the organisms used for baseline calculation (in this case, trophic position equals 1). A 3.4‰ enrichment of $\delta^{15}N$ was assumed to represent an increase of one trophic position (Vander Zanden and Rasmussen 2001):

$$(2) \quad TP_{It} = \{[\delta^{15}N_{It} - (\delta^{15}N_{\alpha\text{baseline}} \times \alpha + \delta^{15}N_{\beta\text{baseline}} \times \beta + \delta^{15}N_{\gamma\text{baseline}} \times \gamma)]/3.4\} + \lambda$$

Stable isotope procedures and statistics

One-way analyses of variance (ANOVAs) and Tukey's pairwise comparisons ($\alpha = 0.05$) were used to test the significance of shifts among years in trout $\delta^{13}C$ signatures and mean trophic position. Source and mixture variability of stable isotope measurements were accounted for using methodology from Phillips and Gregg (2001) and applying the most conservative (95%) confidence interval. Variability of the C:N ratio of major diet items was tested as a possible source of differential fractionation of ^{15}N (Adams and Sterner 2000).

Stable isotope measurements were performed using a Finnigan MAT Delta Plus continuous-flow elemental analyzer at Cornell University's Boyce Thompson Stable Isotope Facility (Ithaca, New York). Samples with high nitrogen content were compared with a methionine standard ($\delta^{13}C = -25.40\text{‰}$, $\delta^{15}N = -0.81\text{‰}$, 40.25% C, 9.39% N) and samples with low nitrogen content were compared with a burned cabbage standard ($\delta^{13}C = -27.22\text{‰}$, $\delta^{15}N = 0.77\text{‰}$, 41.60% C, 3.35% N). The standard error from the mean of each isotopic run never exceeded 0.15‰ with respect to the standards. All statistical analyses were implemented using SPlus (Insightful Corporation, Seattle, Washington). All means are reported with 2 standard errors from the mean (SEM) unless stated otherwise.

Results

Stable isotope baseline characterization

Baseline stable isotope signatures of littoral $\delta^{13}C$ ($-20.19\text{‰} \pm 0.85\text{‰}$) and $\delta^{15}N$ ($1.64\text{‰} \pm 0.75\text{‰}$) and pelagic $\delta^{13}C$ ($-30.15\text{‰} \pm 1.39\text{‰}$) and $\delta^{15}N$ ($3.27\text{‰} \pm 0.81\text{‰}$) in Little Moose Lake did not vary significantly during the study (ANOVAs: $p = 0.275$, $F = 1.38$, $n = 5$, 4, 13; $p = 0.069$, $F = 3.44$, $n = 6$, 5, 3; $p = 0.677$, $F = 0.40$, $n = 4$, 4, 8; and $p = 0.254$, $F = 1.5$, $n = 10$, 6, 3 for 2000, 2001, and 2002 littoral and pelagic carbon and littoral and pelagic nitrogen, respectively). Thus, individual measurements of organisms collected in 2000, 2001, and 2002 were pooled to more accurately portray the overall baselines of carbon and nitrogen in the littoral and pelagic zones of Little Moose Lake. Profundal carbon and

nitrogen baselines were established for 2002 alone; thus, pooling by year was not necessary.

Baseline pelagic $\delta^{13}C$ ($-30.15\text{‰} \pm 1.39\text{‰}$) and profundal $\delta^{13}C$ ($-29.22\text{‰} \pm 1.30\text{‰}$) were not distinguishable from each other (ANOVA: $p = 0.506$, $F = 0.46$, $n = 14$, 4 for pelagic and profundal organism signatures, respectively). Thus, pelagic and profundal organism signatures were pooled for comparison of littoral carbon signatures with pelagic and profundal carbon signatures. Littoral zone organisms were enriched in $\delta^{13}C$ ($-20.19\text{‰} \pm 0.85\text{‰}$) by comparison with pelagic ($-30.15\text{‰} \pm 1.39\text{‰}$) and profundal ($-29.22\text{‰} \pm 1.30\text{‰}$) organisms (ANOVA: $p < 0.001$, $F = 200.09$, $n = 22$, 18 for littoral and pooled pelagic and profundal organism signatures, respectively; Tukey's pairwise comparison at $\alpha = 0.05$).

Organisms collected from the littoral, pelagic, and profundal regions were increasingly enriched in $\delta^{15}N$ with respect to sampling location. The pelagic and profundal regions were not found to be significantly different in signature (pelagic = $3.27\text{‰} \pm 0.81\text{‰}$ and profundal = $3.61\text{‰} \pm 0.37\text{‰}$) but were found to be significantly enriched in $\delta^{15}N$ when compared with the littoral zone signature (ANOVA: $p = 0.009$, $F = 5.42$, $n = 16$, 19, 4 for littoral, pelagic, and profundal organism signatures, respectively). A Tukey's pairwise comparison ($\alpha = 0.05$) confirmed that pelagic and profundal organism signatures were significantly greater than littoral organism values.

Littoral carbon estimation

Lake trout collected for stable isotope and diet analyses (mean length = 444 ± 7.2 mm) did not show a significant size shift during the study period. A significant increase in lake trout $\delta^{13}C$ was observed from 2000 to 2002 (Fig. 1). Source and mixture variability were incorporated into the isotopic model (Phillips and Gregg 2001), and lake trout $\delta^{13}C$ values increased significantly from -25.9‰ to -24.9‰ ($\pm 0.36\text{‰}$ and 0.20‰ , respectively) concurrent with smallmouth bass removal (ANOVA: $p = 0.032$, $F = 3.50$, $n = 16$, 50, 93 for 2000, 2001, and 2002, respectively; Tukey's pairwise comparison at $\alpha = 0.05$).

Diet analysis

No lake trout collected during 2000 contained fish in their stomachs. In 2001, the proportion of fish (by dry weight) in sampled lake trout stomachs increased from 0% to 5%. The proportion of fish (by dry weight) in sampled lake trout stomachs increased dramatically in 2002 to 74% of the total biomass (Fig. 2). Slimy sculpin were the only fish consumed by lake trout during 2001. Lake trout collected during 2002 contained six fish species (brown bullhead, landlocked Atlantic salmon (*Salmo salar*), pumpkinseed, rainbow smelt (*Osmerus mordax*), smallmouth bass, and slimy sculpin) in their diets (Fig. 2).

Following the bass removal, lake trout shifted from a primarily profundal diet (96% and 83% in 2000 and 2001) to a diet composed of 50% littoral inputs in 2002 (Fig. 3). The 2000 and 2001 diets were composed primarily of chironomids. Various species of zooplankton were also abundant in lake trout diets, but they accounted for a negligible proportion of biomass relative to chironomids. Lake trout diets from 1996 and 1997 consisted of more than 70% profundal

Fig. 1. Points represent lake trout (*Salvelinus namaycush*) $\delta^{13}\text{C}$ ($\text{‰} \pm 2$ SEM) by year. Broken horizontal lines represent the expected equilibrium of lake trout with a diet of 100% prey fish, consisting of fish ranging in total length from 40 to 150 mm (-22.08‰), and the most depleted value of $\delta^{13}\text{C}$ measured for any lake trout evaluated in this study (-27.97‰). The most enriched $\delta^{13}\text{C}$ measured for any lake trout was -22.00‰ and therefore is not shown, as this is nearly identical to the assumed signature of a lake trout with a diet consisting of 100% prey fish.

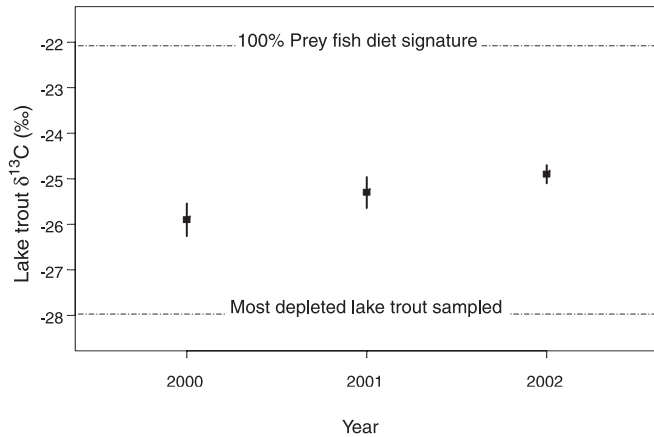
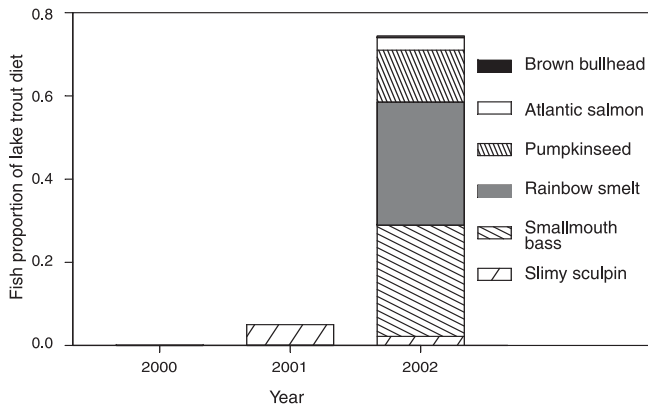


Fig. 2. Annual lake trout (*Salvelinus namaycush*) prey fish diet proportions (by dry weight) from Little Moose Lake. Proportions of brown bullhead (*Ameiurus nebulosus*), Atlantic salmon (*Salmo salar*), pumpkinseed (*Lepomis gibbosus*), rainbow smelt (*Osmerus mordax*), smallmouth bass (*Micropterus dolomieu*), and slimy sculpin (*Cottus cognatus*) consumed are represented by the respective patterns shown.



input, largely chironomids, similar to lake trout in 2000 and 2001. Fish did not comprise a majority of lake trout diet composition until 2002. Stomach fullness (dry weight per individual) for individual lake trout did not vary during the study period (ANOVA: $p = 0.440$, $F = 0.82$, $n = 16, 50, 93$ for 2000, 2001, and 2002, respectively).

Trophic position quantification

The diet-based, three-source-mixing model, using proportions of littoral, pelagic, and profundal inputs to lake trout diets as calculated and displayed in Fig. 3 for 2000, 2001, and 2002, respectively, indicated that lake trout trophic position increased during the smallmouth bass manipulation

Fig. 3. Proportion of lake trout (*Salvelinus namaycush*) diet (by dry weight) made up of prey from littoral (open bars), pelagic (shaded bars), and profundal (solid bars) habitats from Little Moose Lake by year. Numbers within parentheses represent sample size.

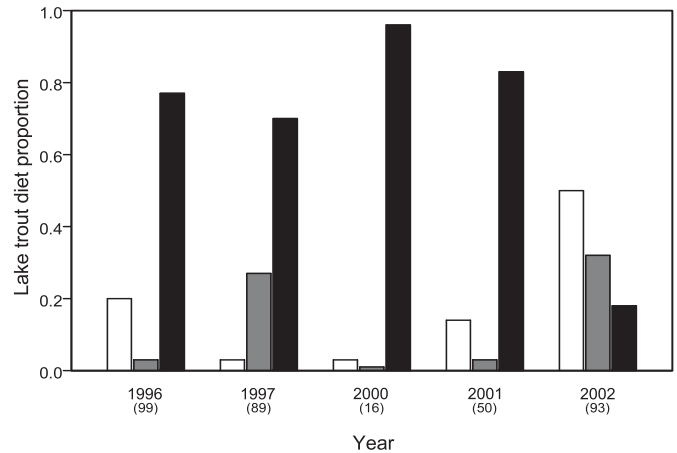
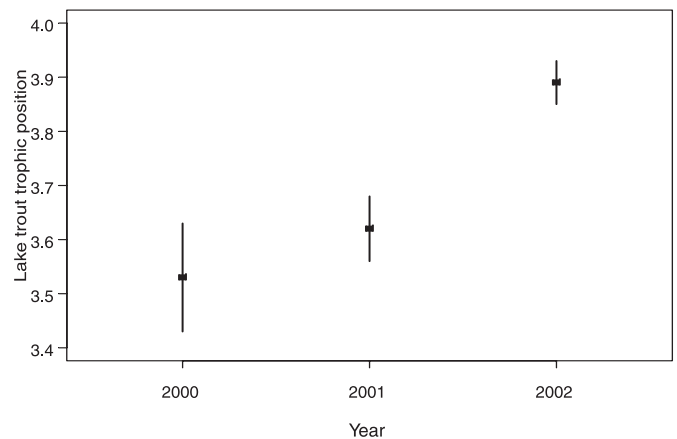


Fig. 4. Annual estimated lake trout (*Salvelinus namaycush*) trophic position (± 2 SEM) for each year of the study.



(Fig. 4). The mean lake trout trophic position in 2000 was 3.5 and then increased significantly to 3.6 in 2001 and 3.9 ($\pm 0.10, 0.06$, and 0.04 , respectively) in 2002 (ANOVA: $p < 0.001$, $F = 71.47$, $n = 16, 50, 93$ for 2000, 2001, and 2002, respectively; Tukey's pairwise comparison at $\alpha = 0.05$). The C:N ratio of major diet items ranged from three to five.

Discussion

Lake trout $\delta^{13}\text{C}$, diet composition, and associated trophic position responded rapidly to smallmouth bass removal within a 2-year period, reflecting food web linkages characteristic of the native fish community. The observed reestablishment of trophic linkages within a native fish community was unexpected for several reasons. Prior to initiation of this study, it was unknown if and how quickly native prey fish could reestablish abundant littoral populations from available refuges associated with Little Moose Lake, such as tributary streams. It was also unclear whether lake trout could rapidly switch from planktivory to piscivory and utilize newly abundant littoral energy sources. Finally, slow growth rates and corre-

sponding slow stable isotope turnover rates were expected to limit our ability to identify a lake trout dietary response to food web changes (Hesslein et al. 1993). Despite these limitations, stable isotope measurements identified a rapid response within the lake food web to the removal of a dominant introduced apex predator. Native prey fish responded quickly to this removal and lake trout took advantage of increased prey fish abundance. Stable isotope turnover rates were likely enhanced by increased growth and metabolism resulting from increased consumption of prey fish (MacAvoy et al. 2001; Harvey et al. 2002). Also, the need to use diet data to account for profundal energy sources increased the rate at which trophic position shifts were detectable.

Lake trout diet data closely corresponded to the recovery pattern observed for prey fish within Little Moose Lake. Increases in prey fish abundance occurred in 2001, 1 year after the smallmouth bass removal was initiated (Weidel 2004), and lake trout quickly switched from a primarily profundal (chironomid) diet to one consisting primarily of littoral inputs. Individual stomach fullness did not vary substantially throughout the removal study, suggesting that the increased prey fish in lake trout diets likely resulted from the substitution of prey fish for invertebrates rather than simply consuming more prey fish in addition to the previous invertebrate diet. The increase in littoral prey fish abundance was similar but larger than what has been seen in other studies of predator-prey interactions involving changes in *Micropterus* populations (Carpenter and Kitchell 1993; Mittelbach et al. 1995).

Ecosystem rehabilitation efforts during the past 30 years have generally focused on chemical measures as metrics for lake restoration (Schindler et al. 1996; Stoddard et al. 1999), while analogous measures for evaluating the success of biotic community restoration have not been well developed (Pimm 1991; Lodge 1993). In ecological studies, the use of stable isotopes has provided an improved ability to understand aquatic food web dynamics. With the use of stable isotope analyses and accurate quantification of baseline isotopic signatures, comparisons across a wide variety of aquatic systems are possible (Post 2002).

Metrics such as growth, abundance, and reestablishment of native species are common measures of lake restoration at a population level; stable isotopes provided an enhanced ability to evaluate the reestablishment of trophic linkages involving complicated interactions between habitat use, fish community, and behavior across disparate systems. Vander Zanden et al. (1999) observed a lake trout stable isotope response 6 years after a lake invasion by smallmouth bass, but precise details regarding the timing of this shift were unavailable. Their observed difference in lake trout $\delta^{13}\text{C}$ values in bass-invaded versus uninvaded lakes (-29.2‰ versus -27.4‰ , difference of 1.8‰ ; Vander Zanden et al. 1999) was comparable with the changes observed in Little Moose Lake lake trout after 2 years of reduced bass abundance (-25.9‰ versus -24.9‰ , difference of 1.0‰) taking into account differences in baseline isotopic values between systems. Also, the mean trophic positions observed by Vander Zanden et al. (1999) for lake trout in lakes where bass were established (3.3) versus lakes where bass were absent (3.9) were similar

to those observed in Little Moose Lake during the lake trout trophic shift in response to bass removal (i.e., from 3.5 to 3.9). These values suggest that food web conditions in Little Moose Lake were restored to a condition similar to systems where bass have not been introduced. Stable isotope and diet data allowed us to quantify a food web recovery as well as compare food web condition and energy input within our study lake with those of other north temperate lakes.

Our study documents a rapid food web response to changes in fish community abundance and reinforces the need to integrate diet and isotope data when evaluating shifts in complicated ecosystems (i.e., three or more disparate energy sources). Typical in many lake systems, Little Moose Lake pelagic and profundal $\delta^{13}\text{C}$ baseline values were indistinguishable; therefore, it was impossible to use only $\delta^{13}\text{C}$ values to differentiate between pelagic and profundal energy sources (Peterson and Fry 1987; Vander Zanden and Rasmussen 1999; Post 2002). Thus, implementation of the three-source-mixing model required establishment of environmental baselines for each energy source incorporated in lake trout diets, and lake trout diet data provided the ability to distinguish between pelagic and profundal invertebrate sources and littoral prey fish (Post 2002).

Two specific concerns could have limited our ability to accurately interpret observed stable isotopic values. First, accurate quantification and assessment of variability in Little Moose Lake isotopic baselines were necessary. The profundal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baselines in our study were established from samples collected exclusively during 2002. Baseline variation is expected and is likely caused by ambient environmental factors that could have changed during the study (Vander Zanden and Rasmussen 1999). However, the profundal baseline was consistent with previous stable isotope measurements in organisms collected from Little Moose Lake in 1999 (Smith 2000) as well as samples subsequently collected during 2003 (J.M. Lepak, unpublished data). Baseline values derived from littoral and pelagic zone invertebrates corresponded to patterns seen in other research, and the isotopic values of longer-lived Little Moose Lake prey fish were also consistent with those of numerous other studies (Vander Zanden et al. 1999; Post 2002). By incorporating error estimates in our isotopic baseline values (Phillips and Gregg 2001), we were able to include both source and mixture variability in our results. Second, differences in C:N ratios of diet items can affect the fractionation of nitrogen. C:N ratios within lake trout diet items ranged from 3 to 5; therefore, we assumed that differential fractionation of ^{15}N was unlikely to have influenced these results because these C:N values were below the ratio at which this influence would be likely to occur (Adams and Sterner 2000).

Little Moose Lake, similar to many lakes in North America, has been exposed to pervasive anthropogenic changes during the past 50 years. The restoration effort reported in this study is broadly applicable to numerous north temperate lake ecosystems because (i) oligotrophic systems dominated by lake trout apex predators were historically common throughout more than 3500 lakes within North America's Northern Hardwood – Boreal transition zone alone (Gunn et al. 2004), (ii) the study lake is comparable in size with the majority of these north temperate lakes (Gunn et al. 2004),

and (iii) the Little Moose Lake fish community is similar to that of many other lakes with limited pelagic forage fish in which resident lake trout populations are particularly vulnerable to littoral predator introductions (Vander Zanden et al. 1999).

Smallmouth bass continue to be widely introduced throughout North America, despite well-documented negative impacts (Whittier and Kincaid 1999; Jackson 2003). Although removal of non-native predators has been implemented to restore lake ecosystems, such efforts have generally involved poisoning the entire fish community and then stocking a small number of native species (e.g., one predator and one prey fish; see Harig and Bain 1998). Efforts to evaluate restoration of lake fish communities have implemented complicated metrics of biotic integrity (Harig and Bain 1998) or have estimated the change in consumption by non-native predators based on the number of removed predators (Ruzycski et al. 2003). We present an alternative approach using stable isotope measurements and diet content analyses to evaluate the restoration of food web linkages in a large lake with a diverse fish community. The observed response was rapid, suggesting that it is possible to remove predators to restore native fish communities and use stable isotopes to measure the reestablishment of lake food web linkages within a recovering fish community.

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