

## Dynamics of Piscivory by Lake Trout following a Smallmouth Bass Invasion: A Historical Reconstruction

YOLANDA E. MORBEY\*<sup>1</sup> AND KRIS VASCOTTO<sup>2</sup>

Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada

BRIAN J. SHUTER

Harkness Laboratory of Fisheries Research, Ontario Ministry of Natural Resources, c/o Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada

**Abstract.**—Our objective was to assess the dynamics of piscivory by lake trout *Salvelinus namaycush* in Lake Opeongo, Ontario, following the introduction of smallmouth bass *Micropterus dolomieu* early in the 1900s. The effects of this introduction on lake trout were thought to be of slight significance at the time, but they may have been obscured by the introduction of cisco *Coregonus artedii* in 1948. Our analyses of lake trout stomach contents and stable isotopes of archived scales indicated that several dietary changes occurred in advance of the cisco introduction. These changes included the consumption of fewer yellow perch *Perca flavescens*, fewer but larger lake whitefish *C. clupeaformis*, and larger lake whitefish for a given lake trout size. Stable isotope analyses were consistent with a decline in the importance of littoral prey for young lake trout before the introduction of cisco. We hypothesize that the indirect effects of smallmouth bass on the pelagic fish community explain these patterns.

The direct and indirect negative impacts of centrarchid basses (*Micropterus* spp. and rock bass *Ambloplites rupestris*) on aquatic communities are becoming increasingly evident. As efficient littoral zone predators, *Micropterus* spp. and *A. rupestris* reduce the diversity and abundance of small-bodied fish species, which forces a change in the community structure of the littoral zone (Chapleau et al. 1997; Whittier and Kincaid 1999; Vander Zanden et al. 1999a; Findlay et al. 2000; MacRae and Jackson 2001). Depletion of littoral prey by *Micropterus* spp. can also affect members of the pelagic community (Jackson 2002). For example, in lakes without pelagic fish prey, introduced smallmouth bass *M. dolomieu* and rock bass caused lake trout *Salvelinus namaycush* to shift from feeding on littoral fishes and benthos to zooplankton

(Vander Zanden et al. 1999a). Lake trout foraging behavior in lakes with pelagic fish present is expected to be affected less by bass invasion because of their minimal dependence on the littoral prey shared with bass (Jackson 2002; Vander Zanden et al. 2004).

Smallmouth bass were introduced into Lake Opeongo before 1920 (Christie 1957), and data on their diet and growth suggest that they progressively depleted the littoral prey during their establishment and early expansion phases (i.e., from about 1936 to 1960; Shuter and Ridgway 2002). Impacts of smallmouth bass on lake trout were thought to be slight because of the contrasting habitat and dietary preferences between species (Martin and Fry 1972). Lake trout fed extensively on lake whitefish *Coregonus clupeaformis* (Martin 1970), a coldwater species with a varied diet that included zooplankton (cladocerans) as a major component at that time (Sandercock 1964). However, impacts of smallmouth bass on lake trout may have been obscured by the introduction of cisco *C. artedii* in 1948, which had pronounced effects on lake trout diet and growth (Martin and Fry 1973; Matuszek et al. 1990). To test whether lake trout were affected by smallmouth bass before the introduction of cisco we examined historical trends in lake trout diet and diet ontogeny.

### Methods

**Lake description.**—Lake Opeongo (45°42'N, 78°22'W) is a large (58.6-km<sup>2</sup>), clear (approximate mean Secchi disc depth = 6 m), oligotrophic lake located in Algonquin Park, Ontario. The lake trout and smallmouth bass angling fisheries on the lake have been surveyed annually since 1936. Descriptions of the creel survey, biology of the lake, lake trout fishery, and aspects of lake trout diet, growth, fecundity, and age at maturity can be found elsewhere (Fry 1949; Martin 1970; Martin and Fry 1973; Shuter et al. 1987; Matuszek et al. 1990). Briefly, most lake trout angled from the lake were measured and their stomach contents were identified, counted, and in some cases, measured for length and weight. In our analyses we

\* Corresponding author: yolanda.morbey@ontario.ca

<sup>1</sup> Present address: Aquatic Research and Development Section, Ontario Ministry of Natural Resources, 1450 7th Avenue East, Owen Sound, Ontario N4K 2Z1, Canada.

<sup>2</sup> Present address: Department of Biology, Laurentian University, 935 Ramsay Lake Road, Sudbury, Ontario P3E 2C6, Canada.

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defined the precisco period as 1937–1950 (insufficient diet data for 1936) to be consistent with previous analyses and to provide a 2-year period between the introduction of the cisco and its subsequent population increase (Matuszek et al. 1990). The postcisco period consisted of the years 1951–1960. No data were available for the period before the smallmouth bass introduction (i.e., before 1920). All these and subsequent analyses were done using SAS version 9.1 (SAS Institute 1990).

*Prey occurrence.*—Multiple logistic regression was used to analyze the temporal variation in prey occurrence among periods (early precisco: 1937–1943; late precisco: 1944–1950; and postcisco: 1951–1960) and between seasons (spring: May; summer: July and August). Diet data collected during other months was excluded because of inconsistent angling effort during these months among years. Separate models were fit to each major fish prey (yellow perch *Perca flavescens* and lake whitefish; cisco occurred in less than 3.8% of lake trout stomachs in any period) and to empty stomachs. The dependent variable was the proportion of lake trout with a particular prey type relative to the number of stomachs examined and the explanatory variables were period, season, and the interaction between period and season. Nonsignificant interaction terms were removed from models before assessing the main effects; significant interaction terms required subsequent univariate analyses to assess the main effects. Lake trout with multiple prey types in their stomachs (yellow perch and lake whitefish:  $n = 316$ ) were represented in two logistic models. In contrast to a previous analysis of the same data, which excluded lake trout with empty stomachs (Matuszek et al. 1990), our approach allowed us to examine possible changes in foraging success. Adjusting for the occurrence of unknown coregonid prey (cf. Matuszek et al. 1990) did not affect our general conclusions (results not shown).

*Diet ontogeny.*—Martin (1970) showed that the size of lake whitefish and yellow perch in the diet of lake trout in Lake Opeongo increased with lake trout size. We extended this analysis to assess temporal variation in these relationships. We used backward stepwise multiple regression analysis to characterize the relationship between prey size and lake trout size. We restricted the analyses to lake trout with fork lengths (FL) between 30 and 70 cm to minimize variation in fork length among years. Although previous studies showed linear relationships between prey size and predator size (Mittelbach and Persson 1998; Keeley and Grant 2001), our preliminary analyses revealed nonlinear patterns. Thus, we tested for the significance of nonlinearities by including second- and third-order

polynomial terms among the candidate independent variables. We used analysis of covariance (ANCOVA) to test for temporal changes in the relationships with time period (1937–1943, 1944–1950, and 1951–1958; insufficient data for 1959 and 1960) as a factor.

*Stable isotope analyses.*—Analysis of naturally occurring stable isotopes is a useful tool for characterizing the diet of lake trout (Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1999a, 1999b; Johnson et al. 2002). For example, the stable carbon isotope ratio ( $\delta^{13}\text{C}$ ) identifies whether dietary carbon was derived from pelagic, littoral, or profundal sources (France 1995; Hecky and Hesslein 1995). In north temperate North America, littoral species generally have greater  $\delta^{13}\text{C}$  values than pelagic species, and profundal species generally have the lowest  $\delta^{13}\text{C}$  values (Vander Zanden and Rasmussen 1999; Vander Zanden et al. 2004). For example, in a study of eight lakes in Ontario, cisco had distinctly lower  $\delta^{13}\text{C}$  values than lake whitefish and lake whitefish had distinctly lower  $\delta^{13}\text{C}$  values than cyprinids (no data for yellow perch; Vander Zanden et al. 2004).

Values of  $\delta^{13}\text{C}$  were measured in archived scales from 79 lake trout ( $\geq 8$  years old) from three sampling periods (1936–1938, 1948, and 1960). In other fish species, values of  $\delta^{13}\text{C}$  from scales and muscle are highly correlated ( $r^2$  values  $> 0.90$ ) with scales showing  $\delta^{13}\text{C}$  enrichment relative to that of muscle (Wainright et al. 1993; Satterfield and Finney 2002; Perga and Gerdeaux 2003). The center of each scale (comprising about two-thirds of the scale radius) was separated from the edge using a piercing needle. This separation of centers and edges allowed us to compare isotopic values early and late in a lake trout's life under the assumption that the fractionation of carbon isotopes does not change with age. Although this assumption was not tested in the current study, the  $\delta^{13}\text{C}$  of walleye *Sander vitreus* muscle was independent of age, length, and weight in Lake Champlain, Vermont (Overman and Parrish 2001). Scales were first washed to ensure that isotope measurements reflected the integrated diet represented by the scale tissue, and not the signature of the mucus, which coats the scale and reflects recent diet. Scales were not washed in a preliminary subset of 15 fish. In a subset of five lake trout, scales were either washed or left unwashed to determine the effect of washing. Perga and Gerdeaux (2003) recommend decalcifying scales with hydrochloric acid (HCl) to remove dissolved inorganic carbon. Although this was not done, values of  $\delta^{13}\text{C}$  from scales with and without HCl treatment were highly correlated in their study ( $r^2 = 0.90$ ), with treated scales showing  $\delta^{13}\text{C}$  enrichment. Stable isotope analyses were done using an Isochrom Continuous Flow Stable Isotope Mass Spectrometer

(Micromass) coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1108) at the Environmental Isotope Laboratory (University of Waterloo, Waterloo, Ontario).

An ontogenetic shift in  $\delta^{13}\text{C}$  value between scale centers and edges was evaluated by repeated-measures analysis of variance (ANOVA) with period as a factor. The  $\delta^{13}\text{C}$  values for scale centers and edges were compared across decades using ANOVA to assess temporal diet shifts in early and late life, respectively. Analyses of variance were followed by analyses of pairwise differences in least squares means to describe the pattern of variation among decades. Comparison of decadal variation assumes that baseline  $\delta^{13}\text{C}$  values did not change over the study period. While this cannot be ruled out, paleolimnological research on Lake Opeongo indicated a relatively stable lower food web structure and, therefore, lake chemistry from before 1800 until 1962 (St. Jacques et al. 2005).

### Results

#### Prey Occurrence

Stomachs were examined in 2,123 lake trout in spring and 7,619 lake trout in summer. Cisco began to increase in occurrence in the diet after 1955 and lake whitefish almost disappeared as a prey item by about 1960. The proportion of lake trout with empty stomachs differed between seasons and among periods (overall model: Wald  $\chi^2 = 496.7$ ;  $df = 3$ ;  $P < 0.0001$ ,  $R^2 = 0.06$ ; Figure 1A). The odds of having an empty stomach were 2.8 times greater in the summer than in the spring (season effect: Wald  $\chi^2 = 224.2$ ;  $df = 1$ ;  $P < 0.0001$ ). The odds of having an empty stomach were 2.1 times greater in 1944–1950 than in 1937–1943 and 1.3 times greater in 1951–1960 than in 1944–1950, reflecting an increase in empty stomachs over time (period effect: Wald  $\chi^2 = 289.9$ ;  $df = 2$ ,  $P < 0.0001$ ; all pairwise contrasts:  $P < 0.0001$ ).

For yellow perch, the two seasons were analyzed separately because the pattern of decadal variation differed between seasons (period  $\times$  season interaction: Wald  $\chi^2 = 103.9$ ;  $df = 2$ ;  $P < 0.0001$ ; Figure 2B). In spring, the proportion of lake trout with yellow perch decreased over the three periods (period effect: Wald  $\chi^2 = 52.9$ ;  $df = 2$ ;  $P < 0.0001$ ;  $r^2 = 0.03$ ; pairwise contrasts:  $P < 0.002$ ). The odds of having a yellow perch in the stomach of a lake trout were 1.5 times greater in 1937–1943 than in 1944–1950 and 1.9 times greater in 1944–1950 than in 1951–1960. In summer, the proportion of lake trout with yellow perch showed a stronger decrease over the three periods than it did in spring (period effect: Wald  $\chi^2 = 778.9$ ;  $df = 2$ ;  $P < 0.0001$ ;  $r^2 = 0.11$ ; pairwise contrasts:  $P < 0.0001$ ). The odds of having a yellow perch in the diet were 2.4

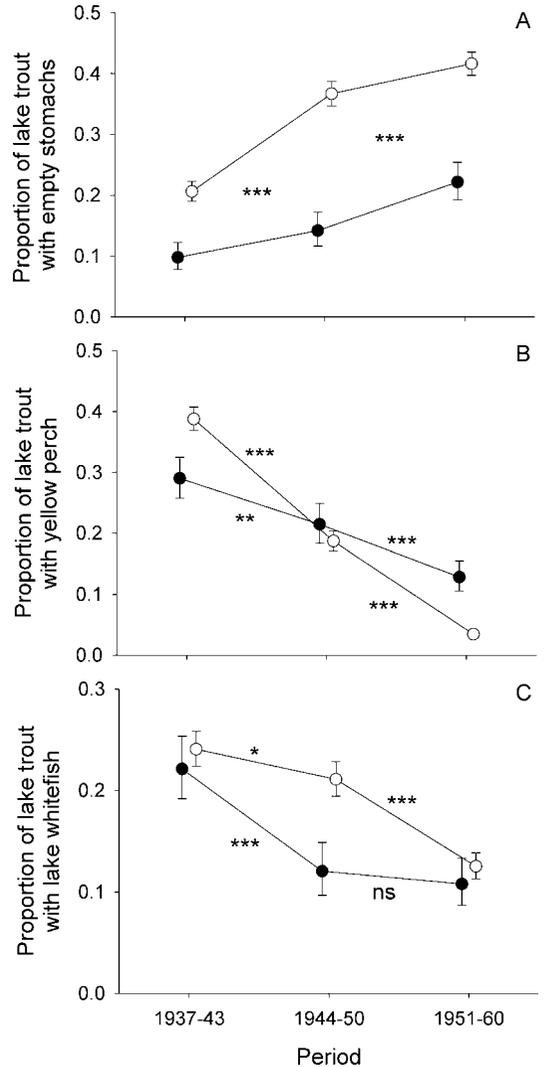


FIGURE 1.—Decadal variation in the proportion of lake trout with (A) empty stomachs, (B) yellow perch, and (C) lake whitefish in spring (solid circles) and summer (open circles); whiskers represent 95% confidence intervals. Significant pairwise differences between consecutive periods (1937–1943, 1944–1950, and 1951–1960) are represented by asterisks ( $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.0001^{***}$ ); ns = not significant. In panel (A), pairwise differences between periods are shown for the two seasons combined; in panels (B) and (C), pairwise differences between periods are shown for the two seasons separately.

times greater in 1937–1943 than in 1944–1950 and 4.2 times greater in 1944–1950 than in 1951–1960.

For lake whitefish, the two seasons were analyzed separately because the pattern of decadal variation differed between seasons (period  $\times$  season interaction: Wald  $\chi^2 = 11.7$ ;  $df = 2$ ;  $P < 0.003$ ; Figure 2C). In

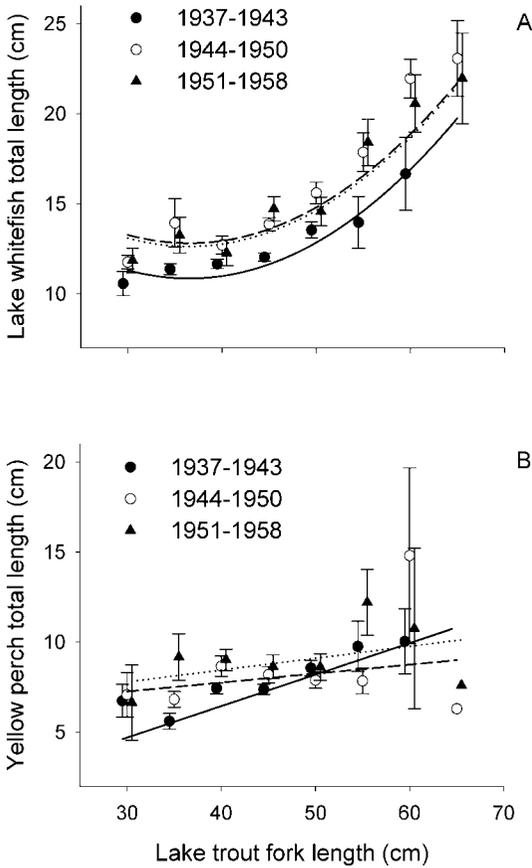


FIGURE 2.—Prey length (means  $\pm$  SEs) versus lake trout fork length (5-cm bins) for (A) lake whitefish and (B) yellow perch during 1937–1943 (solid line), 1944–1950 (dashed line), and 1951–1958 (dotted line). The best-fitting function is shown for each period. Points are offset to facilitate the comparison of standard errors.

spring, the proportion of lake trout with lake whitefish in the stomach was greater in 1937–1943 than in 1944–1950 and 1951–1960 (period effect: Wald  $\chi^2 = 39.9$ ;  $df = 2$ ;  $P < 0.0001$ ;  $r^2 = 0.02$ ; pairwise contrasts: 1937–1943 versus 1944–1950,  $P < 0.0001$ ; 1937–1943 versus 1951–1960:  $P < 0.0001$ ; 1944–1950 versus 1951–1960:  $P = 0.477$ ). The odds of having a lake whitefish were 2.1 times greater in 1937–1943 than in 1944–1950 and 2.4 times greater in 1937–1943 than in 1951–1960. In summer, the proportion of lake trout with lake whitefish in the stomach decreased over the three periods (period effect: Wald  $\chi^2 = 112.8$ ;  $df = 2$ ;  $P < 0.0001$ ;  $r^2 = 0.02$ ; pairwise contrasts:  $P < 0.016$ ). The odds of having a lake whitefish were 1.2 times greater in 1937–1943 than in 1944–1950 and 1.9 times greater in 1944–1950 than in 1951–1960.

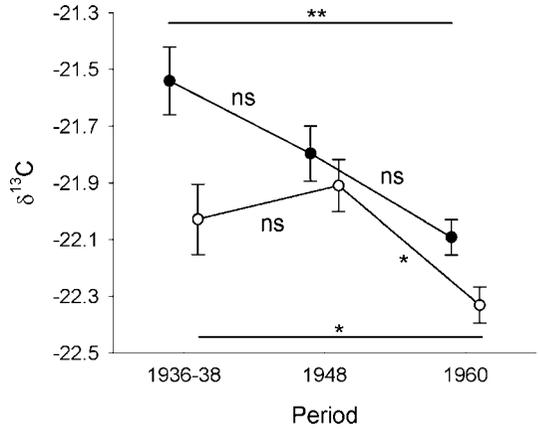


FIGURE 3.—Values of  $\delta^{13}C$  (means  $\pm$  SEs) for the scale centers (solid circles) and scale edges (open circles) in 1936–1938, 1948, and 1960. Significant pairwise differences between consecutive periods (connected by lines) and between 1936–1938 and 1960 (upper horizontal line, scale centers; lower horizontal line, scale edges) are represented by asterisks ( $P < 0.05^*$ ,  $P < 0.01^{**}$ ); ns = not significant.

*Lake Trout Diet Ontogeny*

Large lake trout consumed large lake whitefish and the relationship between their sizes was best described by a quadratic function (statistics for full model with no significant interactions:  $F = 85.5$ ;  $df = 4, 1006$ ;  $P < 0.0001$ ;  $R^2 = 0.25$ ; Figure 2A). For their size, lake trout consumed larger lake whitefish after 1943 than before (period effect:  $F = 24.81$ ;  $df = 2, 1006$ ;  $P < 0.0001$ ). The shape of the relationship between yellow perch size and lake trout size differed among periods (period  $\times$  FL<sup>2</sup> interaction:  $F = 3.85$ ;  $df = 2, 659$ ;  $P = 0.022$ ). When periods were analyzed separately, large lake trout consumed significantly larger yellow perch during 1937–1943 (linear regression:  $t = 5.47$ ;  $df = 411$ ;  $P < 0.001$ ), but not during the later periods ( $P > 0.18$ ; Figure 2B).

*Stable Isotope Analyses*

The comparison of  $\delta^{13}C$  values between scale centers and edges was consistent with an ontogenetic diet shift from littoral to pelagic or profundal prey, but the effect was not significant in all decades (repeated measures ANOVA, decade  $\times$  individual interaction:  $F = 5.24$ ;  $df = 2, 76$ ;  $P = 0.007$ ; Figure 3). Scale centers had greater  $\delta^{13}C$  values compared with scale edges in 1936–1938 (paired  $t$ -test:  $t = 5.28$ ;  $df = 32$ ;  $P < 0.0001$ ) and 1960 ( $t = 4.33$ ;  $df = 22$ ;  $P = 0.0003$ ), but not in 1948 ( $t = 1.22$ ;  $df = 22$ ;  $P = 0.2342$ ). Moreover, the magnitude of the ontogenetic shift in  $\delta^{13}C$  differed among decades ( $F = 5.24$ ;  $df = 2, 76$ ;  $P = 0.007$ ). Based on significant pairwise differences in least squares

means the difference in  $\delta^{13}\text{C}$  between the scale center and edge was greater in 1936–1938 than in both 1948 ( $P = 0.003$ ) and 1960 ( $P = 0.042$ ). Washed and unwashed scales had similar  $\delta^{13}\text{C}$  values for scale edges (paired  $t$ -tests:  $P > 0.5$ ) but scale centers had greater values of  $\delta^{13}\text{C}$  when washed ( $-21.44 \pm 14\%$  [mean  $\pm$  SD]) than when unwashed ( $-21.68 \pm 0.10\%$ ;  $t = 6.00$ ;  $df = 4$ ;  $P = 0.004$ ). This apparent contamination of scale centers by mucus did not obscure the general ontogenetic pattern.

Values of  $\delta^{13}\text{C}$  in the scale centers differed among decades (ANOVA:  $F = 7.22$ ;  $df = 2, 76$ ;  $P = 0.001$ ;  $r^2 = 0.16$ ; Figure 3) and showed a linear decrease (linear contrast:  $F = 14.40$ ;  $df = 1, 76$ ;  $P = 0.0003$ ) with a significant pairwise difference in least squares means between 1936 and 1938 and 1960 ( $P = 0.0003$ ). Values of  $\delta^{13}\text{C}$  in the scale edges also differed among decades ( $F = 3.70$ ;  $df = 2, 76$ ;  $P = 0.029$ ;  $r^2 = 0.09$ ; Figure 3). Based on significant pairwise differences in least squares means,  $\delta^{13}\text{C}$  was greater in 1936–1938 than in 1960 ( $P = 0.045$ ) and greater in 1948 than in 1960 ( $P = 0.011$ ). Individual variation in  $\delta^{13}\text{C}$  values could not be attributed to differences in fork length, weight, or age (linear regression analyses;  $P > 0.09$ ).

### Discussion

The occurrence of yellow perch in the diet of lake trout declined before the introduction of cisco (see Martin 1970). Given the parallel increase in the proportion of lake trout with empty stomachs and the decrease in the proportion of lake trout with invertebrate prey (Martin 1970), this change suggests an increasing scarcity of yellow perch rather than prey switching by lake trout. Direct predation by smallmouth bass probably does not explain the decline in yellow perch. During 1937–1960, the smallmouth bass caught in the fishery (July–September) mostly preyed upon crayfish (Cambaridae) and ate only small quantities of benthic invertebrates, minnows (Cyprinidae), yellow perch, and coregonids (Ontario Ministry of Natural Resources, unpublished data). Moreover, yellow perch and smallmouth bass often co-occur in lakes (MacRae and Jackson 2001). Instead, smallmouth bass may have affected yellow perch indirectly through transfer of nonnative parasites (Martin and Fry 1972) or competition for shared prey (e.g., macroinvertebrates). Other reasons for the declining occurrence of yellow perch are also possible, but cannot be evaluated without additional data.

The occurrence of lake whitefish in the lake trout diet also began to decline before the introduction of cisco, particularly in the spring. Concomitant with this change was an increase in lake whitefish size and a pattern whereby lake trout began to consume larger

lake whitefish for their size. We suggest that before the cisco introduction the availability or accessibility of small lake whitefish declined, forcing lake trout to prey upon larger lake whitefish. Several hypotheses for a decline in small lake whitefish availability can be proposed. For example, smallmouth bass may have affected small lake whitefish indirectly through competition for shared macroinvertebrate prey. The earlier reduction in the occurrence of lake whitefish in the spring rather than in the summer could be explained if niche overlap between smallmouth bass and small lake whitefish was greater in the spring.

The stable isotope data are consistent with some of the dietary changes that occurred in advance of cisco. Younger lake trout, represented by data from the scale centers, shifted towards a diet lower in  $\delta^{13}\text{C}$  between 1936 and 1960. This is consistent with a dietary shift away from littoral prey (e.g., cyprinids, macroinvertebrates, and possibly yellow perch) towards pelagic prey (initially lake whitefish and later cisco). A shift towards lower  $\delta^{13}\text{C}$  could also reflect increased consumption of profundal prey, but this would not be consistent with the stomach content analysis. The  $\delta^{13}\text{C}$  values in older lake trout, represented by data from the scale edges, suggest an increase in the contribution of pelagic prey after 1948, possibly reflecting an increase in the consumption of cisco. In contrast, the declining occurrences of yellow perch and lake whitefish in the lake trout diet between 1936–1938 and 1948 was not accompanied by any significant change in the  $\delta^{13}\text{C}$  of scale edges. However, stable isotope analyses may not always reflect observed shifts in diet, especially when prey items do not have distinct stable isotope signatures. A reasonable possibility is that  $\delta^{13}\text{C}$  signatures for yellow perch and lake whitefish were similar during the study period. If so, the decrease in  $\delta^{13}\text{C}$  among young fish from 1936–1938 to 1948 may be more attributable to the declining importance of cyprinids and macroinvertebrates than to the declining importance of yellow perch. A full interpretation of the lake trout stable isotope data would require stable isotope information from each prey species collected during the 1937–1960 study period.

Lake trout experienced significant dietary changes before the introduction and population expansion of cisco in Lake Opeongo. We hypothesize that smallmouth bass contributed to the observed changes through indirect effects on yellow perch and lake whitefish. While alternative explanations are certainly possible we can think of none with similar explanatory power. Our results suggest that smallmouth bass may affect lake trout when available fish prey with the capacity for zooplanktivory (e.g., lake whitefish) also rely on littoral prey.

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