Where Did They Come From?

Natural Chemical Markers Identify Source and Date of Lake Trout Introduction in Yellowstone Lake

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Fisheries technician Brad Olszewski with a lake trout removed from a Yellowstone Lake spawning area.

EXOTIC SPECIES pose one of the most pervasive threats to fresh waters worldwide (Hall and Mills 2000; Rahel 2000; Kolar and Lodge 2002). Dramatic changes in species abundance and energy flow have been observed following the establishment of a single new species, even in large lakes (Zaret and Paine 1973; Vander Zanden et al. 1999). Although many exotic species have been intentionally introduced for commercial or recreational purposes, unauthorized transplants and invasions have also contributed substantially to exotic species expansion (McMahon and Bennett 1996; Fuller et al. 1999; Rahel 2000).

When an exotic species is first detected in a new location, questions about where it originated and when it was transplanted or invaded are frequently difficult to answer with confidence (Radtke 1995; McMahon and Bennett 1996; Hebert and Cristescu 2002). This uncertainty hinders possible manage-ment actions for avoiding future occurrences and, in some instances, raises questions as to whether a presumed invader is, in fact, native or has resided in the system longer than suspected but at low abundance (Kaeding et al. 1996; Waters et al. 2002). Recent investigations of freshwater zooplankton illustrate the utility of genetic markers as a forensic tool for studying invasion biology (Cristescu et al. 2001; Hebert and Cristescu 2002). In this paper, we demonstrate the use of natural chemical markers in fish otoliths to identify the probable source and date of introduction of an exotic fish species.

Exotic lake trout (*Salvelinus namaycush*) were discovered in Yellowstone Lake in 1994 (Kaeding et al. 1996). This 250,000-ha, high-elevation lake near the headwaters of the Yellowstone River drainage is one of the largest relatively intact lake ecosystems in the United States, and is the primary remaining habitat for Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*)

(Gresswell and Varley 1988). The clear, deep, cold waters and abundant prey base of Yellowstone Lake provide prime habitat for piscivorous lake trout, and by 1996 their population was estimated to be several thousand, including individuals as large as 91 cm in length (Ruzycki et al. 2003). Development of an abundant lake trout population was anticipated if left unchecked, with the resultant high predation pressure causing a significant decline in the Yellowstone cutthroat trout population (Varley and Schullery 1995; Ruzycki et al. 2003). Cutthroat trout generally evolved in the absence of competing top predators (Behnke 1992), and declines have been documented in several western North American lakes following lake trout introduction (Cordone and Frantz 1966; Marnell 1988; Donald and Alger 1993). Consequently, an aggressive lake trout removal program was initiated in Yellowstone Lake in 1995 to protect a valuable recreational fishery and the integrity of the lake's terrestrial and aquatic foodwebs, which are heavily dependent on cutthroat trout (Varley and Schullery 1995; Koel et al. 2003).

The origin of the lake trout in Yellowstone Lake is unknown. Although lake trout from the Great Lakes were introduced into Yellowstone National Park's Shoshone and Lewis lakes in the late 1800s and later spread to Heart Lake, these lakes are in the Snake River (Pacific) drainage, and lack connection to the Yellowstone River (Atlantic) drainage (Fig. 1) (Varley and Schullery 1983). Prior to 1994, no lake trout had been reported in Yellowstone Lake despite extensive population sampling and angler survey records dating back more than 50 years (Gresswell and Varley 1988; Kaeding et al. 1996). Based on the age and size of lake trout when they were discovered in 1994 (≤ 5 years and 43 cm), it was estimated that lake trout had reproduced in Yellowstone Lake since at least 1989, but when the original transplant occurred was unknown (Kaeding et al. 1996).

We used chemical analysis of otoliths (ear stones associated with hearing and balance, composed primarily of calcium carbonate and an organic matrix) to estimate where the lake trout originated and when they were transplanted into
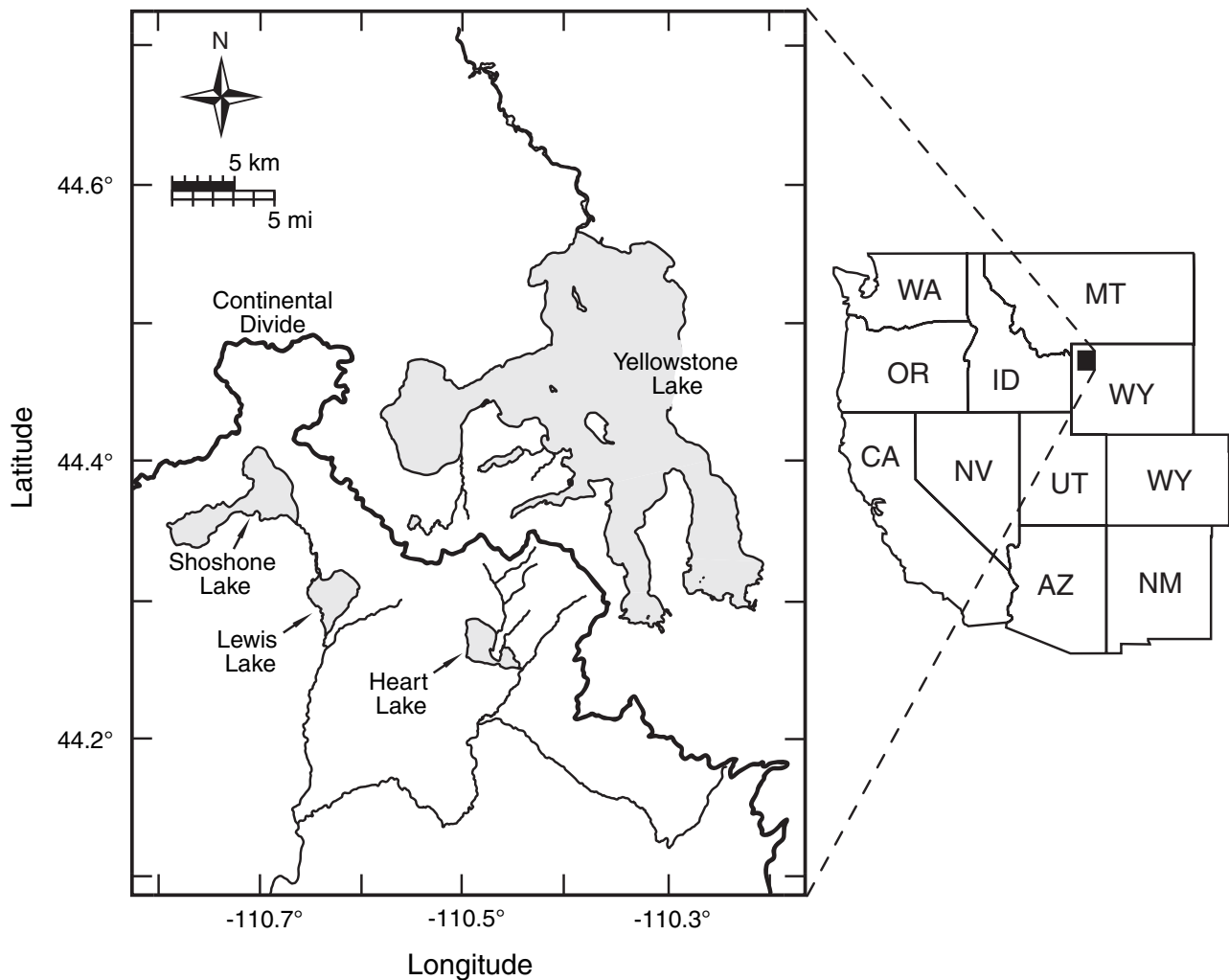

Figure 1. Map of the major lakes in the study area, Yellowstone National Park.

Group	Lake	n	Total length (mm) Median	Total length (mm) Range	Age (years) Median	Age (years) Range	Year-class range
Known-origin	Heart	10	490	327–691	15	8–22	1977–1991
	Lewis	10	503	416–949	14	9–26	1973–1990
	Yellowstone	10	720[a]	700–767	9	8–11	1988–1991
Suspected transplants	Yellowstone	20	805	765–890	18	10–32	1965–1987

[a]Length data were not available for five of the known-origin Yellowstone Lake fish.

Table 1. Summary of length, age, and year-class of the known-origin lake trout and suspected transplants collected from three lakes in Yellowstone National Park.

Yellowstone Lake. Because trace elements of ambient waters are incorporated into otoliths as a fish grows, analysis of natural chemical markers in otoliths can be used to reconstruct environmental history, including timing of movements and stock origins (Campana 1999; Limburg et al. 2001; Thorrold et al. 2001). However, to our knowledge, no one has used the elemental composition of otoliths to assess introductions of exotic species.

The strontium-to-calcium ratio (Sr:Ca) has been the most widely used marker in otolith composition studies because (i) of the strong correlation between otolith and ambient water ratios, (ii) a strontium ion can replace a calcium ion in the calcium carbonate ($CaCO_3$) of the otoliths to form strontium carbonate ($SrCO_3$), and (iii) Sr is more apt to reflect environmental concentrations than other elements owing to a lack of physiological regulation (Campana 1999). Organisms do not actively regulate Sr uptake like other needed elements (e.g., Ca, K, Na, P) or try to regulate against uptake, such as with toxic elements like heavy metals. However, because the uptake is through several membrane barriers (water – gills – blood – endolymph [fluid that bathes the otoliths] – otolith) the concentration is not the same as in the water; there is some filtration. Although similar, Ca and Sr ions are physically different; Sr is larger and heavier. Furthermore, other physical and chemical factors can alter the incorporation of Sr into the otolith during crystal formation. However, as seen in Fig. 3, there is a relation between the ratio of the concentration of Sr and Ca in the source water and what is eventually incorporated into the otolith. In essence, it is almost like Sr is coming along for the ride as Ca is taken up and used to make the otoliths.

We compared the Sr:Ca ratios in otoliths from suspected transplants with those in (i) otoliths of lake trout from more recent year-classes, thought to have been spawned and reared in Yellowstone Lake, and (ii) otoliths of lake trout from Lewis and Heart lakes, the two most likely source lakes in Yellowstone National Park. We hypothesized that lake trout reared in a single lake would have similar otolith Sr:Ca ratios throughout their lives, from the early-growth zone near the nucleus to the outer edge. In contrast, we predicted that lake trout transplanted into Yellowstone Lake would have a significantly different chemical composition between the two zones, reflective of a change in environmental history, and that the Sr:Ca ratio of the early growth zone could be used to identify the probable source lake of the transplant. We further surmised that among suspected transplants, the timing of the change in Sr:Ca ratio in relation to the age of the fish could provide an estimated date of when transplantation had occurred.

Materials and methods

Otolith collection and preparation

Two groups of otoliths were analyzed for this study. The first group consisted of archived otoliths from lake trout that had been collected from Yellowstone Lake during early stages of the lake trout removal program in 1996 and 1997. It was surmised that the largest fish in these samples were likely some of the original fish transplanted to Yellowstone Lake, and smaller sizes were offspring of these suspected transplants. Twenty otoliths, 10 from each year, were randomly selected from among the 164 largest lake trout that constituted the suspected transplant group. These fish were >70 cm total length and comprised the upper 10 to 20% of length range of lake trout collected during 1996 and 1997 gillnet sampling (Table 1). The second group consisted of otoliths from lake trout of known origin: suspected offspring of the original founding population in Yellowstone Lake and lake trout of various ages from Heart and Lewis lakes (Table 1). Otoliths from this group were randomly selected from fish gillnetted in 1999 from all three lakes (n = 10 for each lake).

Otoliths were extracted, cleaned, and stored in polyethylene vials soon after collection. One otolith from each fish was sectioned, ground, and polished to expose the nucleus following the techniques of Secor et al. (1992). Prior to chemical analysis, otolith sections were ultrasonically cleaned in a series of baths of Milli-Q water, analytical-grade hexane, and analytical-grade methanol (<1 min each) to remove surface contaminants.

Otolith chemistry

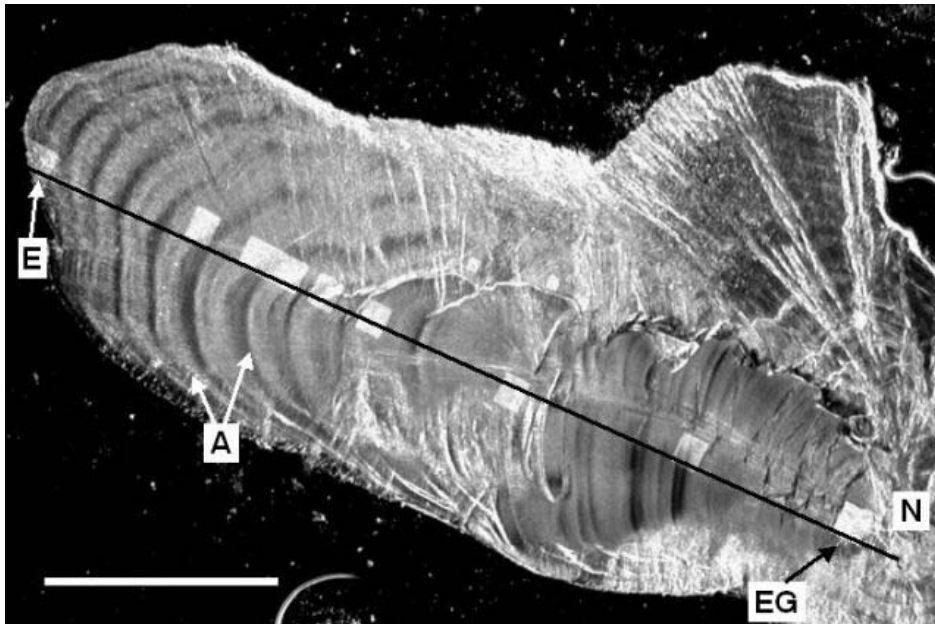Otolith chemical composition was measured with a

Figure 2. Transverse section of a lake trout otolith from a suspected transplant into Yellowstone Lake. Analysis sites for ^{88}Sr and ^{44}Ca ion counts were located in the early-growth zone (EG), near the nucleus (N), and the edge zone (E) in each otolith. Analyses along a transect were used to pinpoint the location of any temporal changes in Sr:Ca ratios. A, annuli. Scale bar = 0.5 mm.

Phi–Evans time-of-flight secondary ion mass spectrometer (ToF-SIMS) (Schueler 1992). For each otolith, ^{88}Sr and ^{44}Ca ion counts were measured at two sites, the early-growth zone near the nucleus and a zone near the outer edge (Fig. 2), and reported as Sr:Ca ratios. For a subset of otoliths from each group (suspected transplants into Yellowstone Lake, $n = 5$; offspring of transplants, $n = 1$; Heart Lake, $n = 2$; Lewis Lake, $n = 1$), additional ion counts were measured at three equidistant points between the early-growth and edge sample sites. If large changes were detected between adjacent sample sites, further sites were sampled to pinpoint the location of temporal changes in Sr:Ca ratio along the otolith axis (Fig. 2). Abrupt changes in Sr:Ca ratio have been correlated with rapid changes in water chemistry (e.g., Limburg et al. 2001). The date of a large change in Sr:Ca ratio, indicative of a movement to new waters, was estimated by comparing the location of the change on the otolith axis with the age of the fish at that time. Annuli were identified using aging criteria developed for lake trout otoliths by Sharp and Bernard (1988).

Water chemistry

Sr:Ca ratios of water from each of the three study lakes were measured to assess whether geochemical differences existed among the lakes, and the degree to which these differences were imparted to lake trout otoliths. Surface water samples were collected from Heart and Lewis lakes in 2000 ($n = 4$ per lake) following standard protocols (American Public Health Association 1998). Water was collected in 1-L poly-

ethylene acid-washed bottles, and 100 mL of each sample was immediately filtered through a 0.45-µm-pore membrane filter into an opaque, acid-washed polyethylene bottle. Water samples were then preserved with 1 mL of analytical-grade concentrated nitric acid and refrigerated until analyzed. Yellowstone Lake water samples were collected at different depths in the water column in four areas of the lake (Southeast Arm, West Thumb, Mary Bay, and Stevenson Island) in 1997 ($n = 30$) and 1998 ($n = 41$) using a hydrobottle clean of trace metals (Balistrieri et al. in press). The water samples were filtered and preserved using the same methods described above. Total dissolved Sr and Ca concentrations (milligrams per liter) were measured with a Perkin-Elmer Sciex Elan 6000 inductively coupled plasma mass spectrometer (Lamothe et al. 1999) and converted to molar concentrations for calculation of the Sr:Ca ratio.

Statistical analyses

A type III mixed model analysis of variance (ANOVA) and Tukey's multiple comparison tests (SAS Institute Inc. 2000) were used to compare Sr:Ca ratios among known-origin lake trout from Heart, Lewis, and Yellowstone lakes. Lake and otolith zone (early growth and edge) were included as fixed factors, and individual fish, zone × fish interaction, and zone replication as random factors in the ANOVA. For all tests, significance was measured at $\alpha = 0.05$.

Nearest-neighbor discriminant analysis was used to determine the probable source of lake trout in Yellowstone Lake. In this type of analysis, each new observation is assigned to the group to which the majority of its nearest neighbors belong (Johnson 1998). Mean otolith Sr:Ca ratios for known-origin fish, weighted by number of sites sampled in each otolith zone, were used to construct the model. The Sr:Ca ratios from lake trout otoliths of suspected transplants were classified using the model developed for the known-origin data set.

Differences in lake water Sr:Ca ratio among the three study lakes were evaluated using a one-factor ANOVA, and Tukey's multiple comparison test was used to test for pairwise differences. Simple linear regression was used to assess the relationship between otolith and lake water Sr:Ca ratio. Only Sr:Ca data from the otolith edge zones were used to best match otolith composition with lake water composition at the times

of sampling (within one year for Heart and Lewis lakes and two years for Yellowstone Lake).

Results

Lake water Sr:Ca ratios were significantly different among Heart, Lewis, and Yellowstone lakes, with differences in mean values among the lakes ranging from 160% to 270% (Fig. 3; Table 2). Tukey's multiple comparison tests indicated significant differences for all pairwise comparisons among the lakes. There was a significant linear relation between the otolith Sr:Ca ratios of known-origin lake trout and the lake water Sr:Ca ratios (Fig. 3). Although water samples from Lewis and Heart lakes were collected in a different year than were Yellowstone Lake samples, the small differences in lake water Sr:Ca between the 1997 and 1998 samples in Yellowstone Lake suggest that annual variation in water chemistry was minor compared to the among-lake differences (Table 2).

Otolith Sr:Ca ratios of known-origin lake trout were also significantly different among the three lakes (Fig. 4). Mean otolith Sr:Ca ratios of Yellowstone Lake lake trout were significantly different from lake trout otolith Sr:Ca ratios from Heart Lake and Lewis Lake. Differences in otolith Sr:Ca ratios between lake trout from Lewis and Heart lakes were not significant at the $\alpha = 0.05$ level. However, the Sr:Ca ratio for Lewis Lake fish was strongly influenced by one fish with a Sr:Ca ratio much greater than that observed in the other nine fish sampled (Fig. 4). When this outlier was removed, the pairwise difference in otolith Sr:Ca ratios between Lewis Lake and Heart Lake lake trout was highly significant.

Otolith Sr:Ca ratios between the early-growth and edge zones among known-origin lake trout from each lake varied little (Fig. 4), the average difference ranging from 0.1 to 5.3%, despite a wide range in the age of fish sampled (8–26 years) (Table 1). Variation of Sr:Ca ratios obtained from multiple sampling within a sample site on the otolith was also low, averaging 3.92% ($n = 25$). Accordingly, there was no significant interaction between lake and otolith zone as factors in the ANOVA. Additional samples taken between the early-growth and edge zones also revealed consistent Sr:Ca ratios across the otolith growth axis among lake trout sampled from different lakes (Fig. 5). Nearest-neighbor discriminant analysis correctly classified 90–100% of lake trout into their home lake (Table 3).

In sharp contrast with lake trout of known origin, 18 of

Lake	Year	n	Mean (SD)
Heart	1999	4	2.40 (0.23)
Lewis	1999	4	1.53 (0.71)
Yellowstone	1997	30	3.92 (0.10)
	1998	41	4.01 (0.14)

Table 2. Lake water Sr:Ca ratios (mmol·mol^{-1}) from Heart, Lewis, and Yellowstone lakes, Yellowstone National Park.
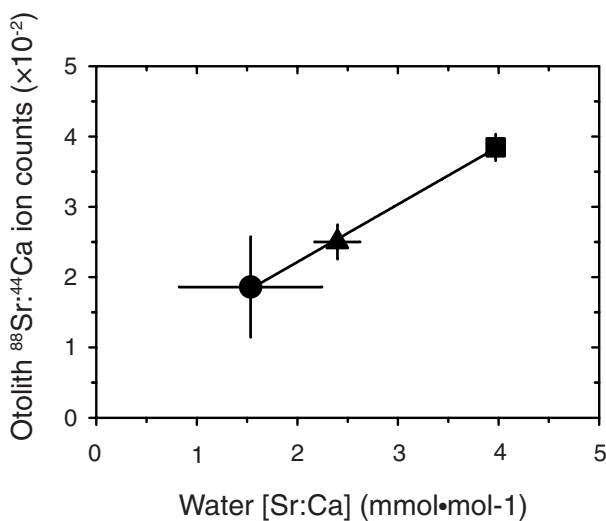

Figure 3. Relation between mean lake water Sr:Ca ratios and mean otolith edge Sr:Ca ratios of lake trout from Heart (▲), Lewis (●), and Yellowstone (■) lakes. The solid line denotes fitted linear regression.
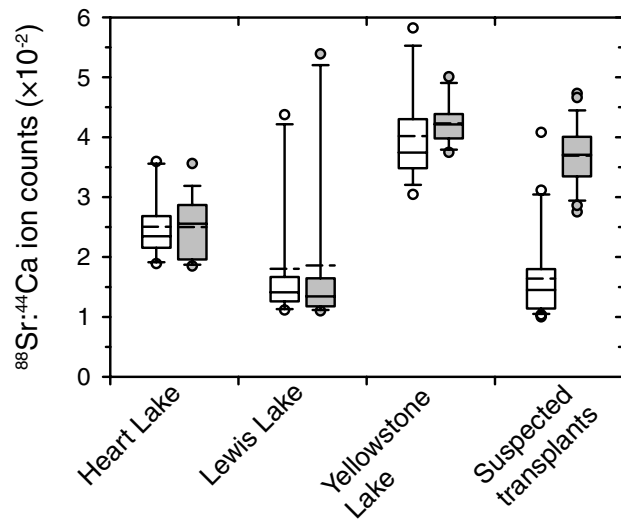

Figure 4. Comparison of Sr:Ca ratios of known-origin lake trout otoliths and otoliths of suspected transplants. Two zones were analyzed for each otolith: early-growth (open boxes) and edge zones (shaded boxes) for both known-origin lake trout from Heart, Lewis, and Yellowstone lakes ($n = 10$ per lake) and suspected transplants gillnetted from Yellowstone Lake ($n = 20$). Boxes show the mean Sr:Ca ratios (broken line), median (central solid line), first and third quartiles (box edges), and individual outliers (circles) outside the 10th and 90th percentiles (whiskers).

20 suspected transplants, ranging in age from 13 to 32 years of age at the time of their collection in 1996 and 1997, exhibited substantial increases (mean = 256%) between the early-growth and edge zones (Fig. 4). Eighty percent of the edge zones of suspected transplants were classified by the discriminant model as Yellowstone Lake, whereas 90% of the Sr:Ca ratios measured in the early-growth zone were classified as Lewis Lake (Table 3). This percentage increased to 100% if the two fish that had similar early-growth and edge zone Sr:Ca ratios were excluded from the classification analysis. Sampling along the otolith axis of a random subset (n = 3) of lake trout exhibiting the abrupt shift in Sr:Ca ratio revealed that Sr:Ca ratio increases occurred within a short period (Fig. 6). The increase in Sr:Ca ratios was estimated to occur in 1989 for two fish (Figs. 6a and 6b) and in 1996 for one fish (Fig. 6c) of the subset sampled. The other two fish, representing the lake trout with similar early-growth and edge zone Sr:Ca ratios, showed little variation in Sr:Ca ratios along the otolith axis (Figs. 6d and 6e). These fish were the youngest in the group of suspected transplants (ages 10 and 11).

Discussion

Our work demonstrates that otolith chemical composition can be used to identify a probable source and date of exotic species introductions. Water chemistry differed significantly among the three large lakes we studied, and these differences were directly imparted to lake trout otoliths. The low variation in Sr:Ca ratios of known-origin lake trout along the otolith axis from the early-growth to the edge zone, despite a wide range of ages, established that lake trout from each lake lived in a similar water chemistry throughout their lives. This temporal and spatial stability in otolith chemical signatures was reflected by the high discriminatory power to classify lake

trout by their home lake based on unique otolith Sr:Ca ratios. These findings corroborate previous work demonstrating (i) a strong association between chemical composition of water and otolith chemistry (Bath et al. 2000; Wells et al. 2003), and (ii) that source waters, even in freshwater environments, can be identified with a moderate-to-high degree of precision based on otolith chemical composition (Thorrold et al. 1998; Wells et al. 2003). Both attributes of otoliths are important in determining stock origins, and our findings indicate that this is particularly relevant for exotic species where stock origin is frequently unknown.

Unlike known-origin lake trout, the large and rapid change in Sr:Ca ratio along the otolith axis of suspected transplants demonstrates that these fish experienced a rapid change in water chemistry. The magnitude of the change in otolith Sr:Ca ratio among suspected transplants (256% increase) mirrors that shown by anadromous fish migrating from freshwater to seawater. For example, Limburg (1995) found that otolith Sr:Ca ratios of age-0 American shad (*Alosa sapidissima*) increased by 250 to 620% during movement from freshwater to
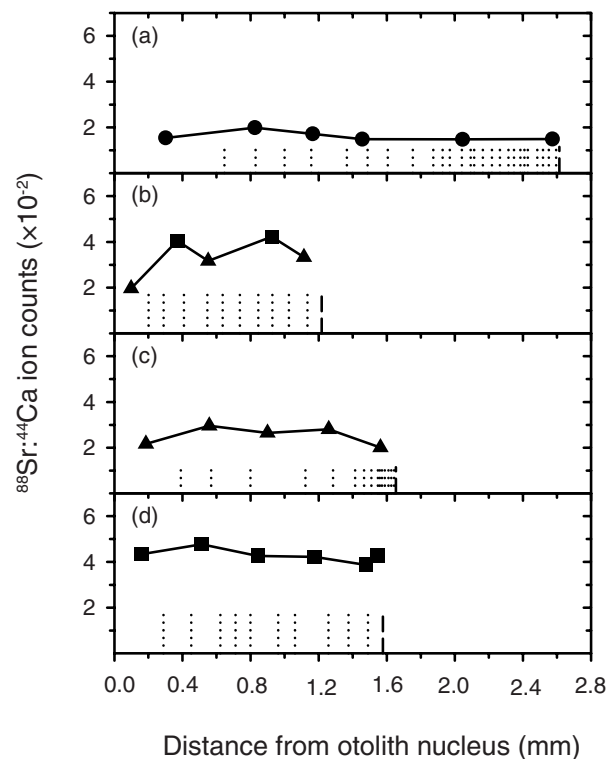

Figure 5. Patterns of Sr:Ca ratios along the otolith axes of four known-origin lake trout from (*a*) Lewis Lake (26 years, 949 mm), (*b*) Heart Lake (10 years, 481 mm), (*c*) Heart Lake (15 years, 490 mm), and (*d*) Yellowstone Lake (10 years, 767 mm). Analysis sites were classified by discriminant analysis: Lewis Lake (●), Heart Lake (▲), and Yellowstone Lake (■). The dotted lines show the location of annuli and the broken line the otolith edge.

seawater. Such a large and rapid change in otolith chemistry among lake trout from older year-classes supports the hypothesis that lake trout were transplanted to Yellowstone Lake. All Yellowstone Lake lake trout from younger age-classes, ≤11 years (1986 estimated year-class and later) at the time of collection in 1996–1999, had similar early-growth and edge zone Sr:Ca ratios, indicating a constant environmental history. In contrast, all lake trout from older year-classes had a marked increase in Sr:Ca ratios between the early-growth and edge zones, indicating that these fish had reared in waters of dis-
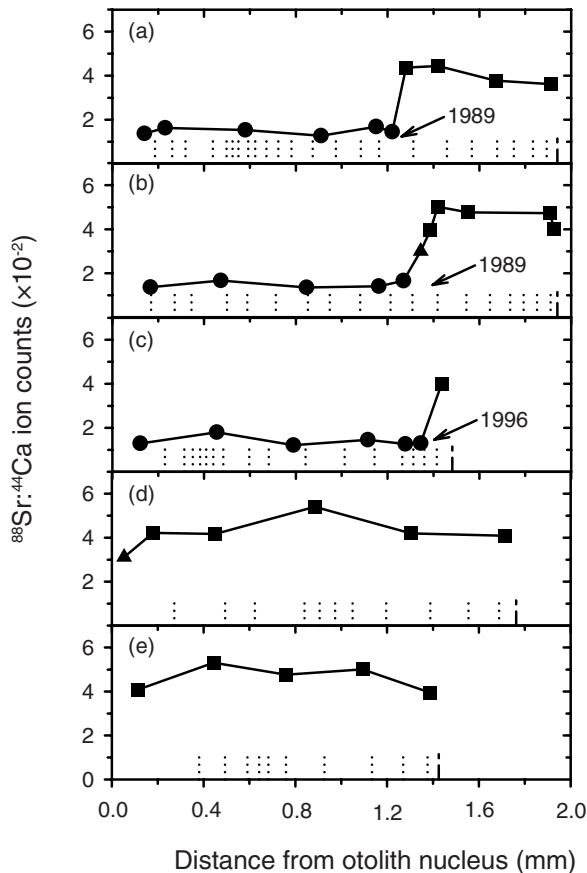

Figure 6. Patterns of Sr:Ca ratios measured along the otolith axes of five lake trout from the group of suspected transplants collected from Yellowstone Lake: (*a*) 23 years, 832 mm, (*b*) 18 years, 850 mm, (*c*) 16 years, 768 mm, (*d*) 11 years, 782 mm, and (*e*) 10 years, 765 mm. Three of the fish show a rapid increase in Sr:Ca ratios corresponding to transplant dates of 1989 (Figs. 6*a* and 6*b*) and 1996 (Fig. 6*c*), whereas the two youngest fish (Figs. 6*d* and 6*e*) show little variation in Sr:Ca ratios, suggesting that they had lived in Yellowstone Lake throughout their lives. Analysis sites were classified by discriminant analysis: Lewis Lake (●), Heart Lake (▲), and Yellowstone Lake (■). The dotted lines show the location of annuli and the broken line the otolith edge. Arrows mark the estimated year that the increase in Sr:Ca ratios occurred.

tinctly different water chemistry during their life-span. These results therefore support the assertion that initial transplanting and natural reproduction of lake trout in Yellowstone Lake likely occurred during the mid- to late l980s (Kaeding et al. 1996). Although our sample size was not large enough to pinpoint the exact number and timing of transplants, Ruzycki et al.'s (2003) estimate of 298 lake trout >10 years old in 1996 (year-class 1986 and earlier) suggests that a rather large number of individuals were transplanted. Moreover, the dating of the abrupt shifts in otolith chemistry as occurring in 1989 and 1996 suggests that multiple transfers may have occurred.

The classification of 90% of the early-growth-zone Sr:Ca ratios of the suspected transplants into Lewis Lake by discriminant analysis suggests that of the two lakes considered to be the most probable source lakes within Yellowstone National Park, Lewis Lake is the likely source of transplanted lake trout. Unlike Heart Lake, Lewis Lake is accessible by road, which may have facilitated the unauthorized transfer of lake trout into Yellowstone Lake.

Change in Sr:Ca ratios with age or maturation (ontogenetic or physiologic effects) is a possible alternative explanation to the transplant hypothesis. However, an age- or maturation-induced Sr:Ca ratio increase was unlikely given that lower Sr:Ca ratios would be expected in the early-growth zone among all lake trout. Further, the pattern of increased Sr:Ca ratio was only observed in suspected transplants and not in the early-growth zone or among younger age groups of other lake trout sampled from Yellowstone Lake or from any of the lake trout sampled from Heart and Lewis lakes, which varied greatly in age.

Another possible explanation for the increase in Sr:Ca ratios in the otoliths of the suspected transplant group of lake trout is temporal or spatial variation in lake water Sr:Ca ratios of Yellowstone Lake. The large increase in otolith Sr:Ca ratios in 1989 observed in some lake trout from the suspected transplant group coincided with the intense wildfires in Yellowstone National Park in 1988 that altered dissolved ion concentrations of some streams in Yellowstone National Park (Minshall et al. 1997). Although Sr was not measured, other dissolved ions in the lake showed only minor changes in concentration, and Lathrop (1994) and Theriot et al. (1997) found no evidence for significant changes in water chemistry resulting from the 1988 wildfires; therefore, temporal changes in water chemistry seem unlikely to account for the 256% increase in otolith Sr:Ca ratios for Yellowstone Lake lake trout. Yellowstone Lake has many hydrothermal vents that may be a source of local enrichment of Sr and Ca (Balistrieri et al. In press). However, we found that lake water Sr:Ca ratios varied little (<3.5%) with depth or among lake subbasins; therefore, it is also unlikely that the increase in otolith Sr:Ca ratios was a result of fish inhabiting different areas within Yellowstone Lake with different Sr:Ca ratios.

There are two important caveats when assessing the

implications of this study. First, the long life-span of lake trout facilitated a long-term retrospective analysis of their environmental history. Detection of unique chemical marks would have been more difficult in species with higher turnover rates or with extensive migrations between waters of differing chemical signatures. Second, although Lewis Lake was identified as the source lake for transplanted lake trout with a high degree of probability, not all ambient waters have unique Sr:Ca signatures (Gillanders et al. 2001; Wells et al. 2003; Munro 2004). Therefore, we cannot eliminate the possibility that lake trout were transplanted from some other lake with Sr:Ca ratios similar to those of Lewis Lake. In future studies, use of isotopes or other elements in addition to Sr could enhance the accuracy of identifying source waters (Kennedy et al. 2002; Wells et al. 2003).

There is growing appreciation for just how extensive introductions of exotic species have been, and the formidable problem they present for aquatic ecosystem management (Hall and Mills 2000; Rahel 2000; Kolar and Lodge 2002). For instance, in Montana alone, 375 cases of unauthorized introductions of fishes of 45 different species have been documented in 224 different waters (Vashro 1995). Detection of an exotic species often poses questions about when the invasion occurred and the geographic origin of the exotic, but few tools have been available to answer them (McMahon and Bennett 1996; Hebert and Cristescu 2002; Waters et al. 2002). Better knowledge of where exotic species originated and the relative risks they pose is essential for the design of educational and regulatory programs to stem the tide of future unauthorized introductions (McMahon and Bennett 1996; Kolar and Lodge 2002). Genetic markers have recently been shown to be a useful forensic tool for studying invasion biology (Cristescu et al. 2001; Hebert and Cristescu 2002; Waters et al. 2002). Our study demonstrates how chemical analysis of otoliths can provide a novel forensic tool to estimate geographic origin and timing of exotic fish introductions. Because both chemical and genetic analysis techniques have distinct advantages and limitations (Cristescu et al. 2001; Thorrold et al. 2001; this study), a combination of both tools could provide important insights into the study of invasion biology.

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Acknowledgements

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