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Application of Otolith Chemistry to Investigate the Origin and State-Straying of Steelhead in Lake Erie Tributaries

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Abstract

In Lake Erie, the fishery for steelhead *Oncorhynchus mykiss* is overwhelmingly dominated by stocking from state agencies in Michigan, New York, Pennsylvania, and Ohio. Managers that stock steelhead may become concerned if a sizeable portion of the fish they stock do not return to the waters in which they were released and instead stray to other states ("state-straying"). During fall 2009, spring 2010, and spring and fall 2015, we evaluated the origin and state-straying of adult steelhead in five annually stocked tributaries of Lake Erie. We also investigated spatial differences in the origin and state-straying of adult steelhead at different stream locations in two tributaries during 2015. Otolith chemistry signatures were first used to discriminate among yearling steelhead from each of the state hatcheries that stock Lake Erie and wild juveniles from Cattaraugus Creek, New York, and the Grand River, Ontario, resulting in a mean jackknifed classification accuracy of 88% (range = 72–100%). Otolith chemistry analysis was then performed on unknown-origin adult steelhead collected in Lake Erie tributaries during the fall and spring spawning runs, and natal sources were identified by using source-specific otolith chemical signatures. State-strays averaged 46% (range = 13–88%) of the adult fish collected, and high percentages of strays were identified in Chautauqua Creek, New York (72%), and Cattaraugus Creek (88%). Steelhead collections in these New York tributaries during a second year revealed that the percentage of strays present was consistently high, and large proportions of strays were identified in both upstream and downstream locations. These results suggest that state-straying is widespread in Lake Erie tributaries and that strays make up a large proportion of New York's Lake Erie tributary fishery. Strategies to reduce straying may include practicing upstream releases and reducing the number of hatchery fish that are released in some states.

[INTRODUCTION]

Homing to natal sites is a basic life history trait of anadromous salmonids that increases the likelihood of successful reproduction for adult fish and the likelihood of survival for juveniles (Hendry et al. 2004; Quinn 2005). Mature fish that spawn in locations other than the sites from which they originated are considered strays (Quinn 1993). Straying is relatively common, and successful reproduction of strays occurs at low levels in salmonid populations (Reisenbichler et al. 1992). Straying allows salmonids to colonize new habitats (Milner and Bailey 1989), avoid locally unfavorable conditions (Leider 1989), maintain genetic diversity (Horrall 1981), and support metapopulations (Hanski and Gilpin 1997). However, fishery managers may be concerned about straying if a sizeable portion of the fish they stock do not return to the waters in which they were released, thus reducing angler catch rates within their management area. Straying can also negatively impact salmonid populations when hatchery fish interbreed with wild individuals, reducing genetic diversity (Emlen 1991; Waples 1991; Adkison 1995; Felsenstein 1997; Chilcote 2003).

In Lake Erie, the fishery for steelhead (anadromous form of Rainbow Trout *Oncorhynchus mykiss*) generates over $19 million in revenue each year for local economies in Michigan, New York, Ohio, Pennsylvania, and the province of Ontario (Murray and Shields 2004; Kelch et al. 2006; P. Reinelt, State University of New York at Fredonia, unpublished data). Although there is some open lake harvest of steelhead in Lake Erie, most fishing pressure occurs through tributary angling that takes place when adult fish return to spawn in tributaries (CWTG 2016). Because natural reproduction is not sufficient to sustain this fishery (Thompson and Ferreri 2002), close to 1.9 million juvenile steelhead are stocked annually into Lake Erie bays and tributaries (CWTG 2016). State fisheries management agencies are responsible for the majority (92%) of all steelhead stocking effort in Lake Erie (2015: Michigan, 64,735 yearlings; Pennsylvania, 1,079,019 yearlings; Ohio, 421,740 yearlings; New York, 1,378 fingerlings and 152,545 yearlings), and approximately 8% of the steelhead stocking is through sportsmen's organizations in Pennsylvania (74,512 yearlings) and Ontario (70,250 yearlings; CWTG 2016; Figure 1).

Each state hatchery system obtains steelhead broodstock from a different source, and the average size at stocking is variable (124–193 mm). Stocking dates and locations (near the mouth versus upstream) also vary by state, year, and tributary. The differential stocking practices used throughout Lake Erie may influence survivorship, spawning site fidelity, and straying of steelhead. Agencies that stock smaller individuals likely have decreased returns, as smaller individuals are much less likely to survive after stocking (Ward 1989; Slaney et al. 1993; Seelbach et al. 1994; Budnik and Miner 2017). <AQ: Ward 1989 is not found in the references.>Additionally, near-mouth stocking or early emigration (i.e., due to high spring discharge events) could cause steelhead to leave a stream before imprinting occurs (Daugherty et al. 2003), leading to increased straying. Along with size and location, the strain of steelhead stocked by each state and the procedures for collecting broodstock may influence survivorship, site fidelity, and the timing of spawning runs (Keefer and Caudill 2014). Different strains of steelhead are stocked by each state surrounding Lake Erie, and broodstock collection procedures vary (multiple-season collections versus spring-only collections). Wild juvenile steelhead that are present in some Lake Erie tributaries may also influence site fidelity by producing pheromones that attract homing adults (Groot et al. 1986; Quinn and Tolson 1986; Courtenay et al. 1997) <AQ: Courtenay et al. 1997 is not found in the references.>and thus could potentially attract straying individuals.

Because considerable effort and resources are invested in stocking, identifying the origin of spawning steelhead is crucial to help inform managers about straying among tributaries and the overall effectiveness of stocking efforts. Straying is traditionally defined as the migration of mature individuals to spawn in a stream other than the stream of origin (Quinn 1993); however, we could not identify straying by site, so instead we focused on straying at the state level (hereafter, “state-straying”). To do this, we used discriminant analysis to identify source-specific elemental chemistry in otoliths of juvenile steelhead, and we used this otolith chemistry to identify the hatchery origin of spawning steelhead in Lake Erie tributaries. The elemental composition of otoliths reflects ambient water chemistry at the time of deposition (Bath et al. 2000; Walther and Thorrold 2006), and otoliths from fish that have experienced elementally distinct waters will record unique signatures reflective of those habitats. In steelhead hatcheries, different water sources are often used at different times of the year to maintain optimal water temperatures. The different water sources used are consistent from year to year (state fish hatchery managers, personal communication) and have been shown to be (1) significantly different elementally and (2) temporally stable (Boehler et al. 2012). Otolith chemistry is a popular and effective method for discriminating among stocks of fish (Campana 1999; Elsdon et al. 2008; Brenner et al. 2012) and has been used widely in the Great Lakes (Pangle et al. 2010; Reichert et al. 2010; Hayden et al. 2011; Marklevitz et al. 2011; Watson 2016). Most notably, it has been demonstrated that the otolith chemistry signatures of steelhead reared at different hatcheries around Lake Erie are significantly different and temporally stable, allowing stocks of steelhead from different year-classes to be accurately discriminated (Boehler et al. 2012).

Although salmonid homing to the river of origin has been extensively documented (Quinn et al. 1989, 2006; Quinn 1993; Dittman et al. 2010; Keefer and Caudill 2014), the fidelity of fish to their natal (or stocked) site is not as well understood (Dittman et al. 2010). The selection of spawning sites likely involves a complex trade-off among selective pressures for homing, spawning habitat selection, competition, and mate choice (Dittman et al. 1996; Hendry et al. 2004). The weighting of these tradeoffs may be different for fish that do not return to their stream of origin (strays). For example, if selective pressures to home are weighted less in straying fish, strays may be expected to be more exploratory and more likely to travel further upstream to find suitable spawning sites. Studies that have focused on the prevalence of salmonid strays at different upstream locations have been contradictory, as a slightly higher proportion of strays was found at upstream locations in a Lake Erie tributary in Pennsylvania (Boehler et al. 2012), whereas the proportions of hatchery Pink Salmon *Oncorhynchus gorbuscha* strays from individual hatcheries in Prince William Sound, Alaska, declined exponentially with upstream distance from a given release site (Brenner et al. 2012). To provide additional information valuable for managers (i.e., identifying exploratory behavior before spawning; and assessing the vulnerability of wild populations to hatchery strays), we sought to determine whether a higher or lower proportion of strays was present at upstream locations.

The objectives of our study were to (1) confirm discrimination among juvenile steelhead from different Lake Erie sources by using otolith chemical signatures; (2) use otolith chemical signatures developed for juvenile sources to predict the origin of adult steelhead returning to spawn in Lake Erie tributaries; (3) evaluate the origin and state-straying of adult steelhead in different Lake Erie tributaries; and (4) evaluate differences in the proportion of state-strays at upstream versus downstream locations in Lake Erie tributaries.

[A]METHODS

[C]*Steelhead collections*.—For stock identification, hatchery yearling steelhead (TL [mean ± SE] = 163 ± 4 mm; range = 63–220 mm) were provided by managers and personnel from state hatchery systems in Lake Erie (Wolf Lake State Fish Hatchery [SFH], Michigan; Castalia SFH, Ohio; Salmon River SFH, New York; and Linesville SFH, Tionesta SFH, and Fairview SFH, Pennsylvania) and from a private hatchery (3-C-U Trout Association's Erie County Cooperative Trout Nursery, Pennsylvania). Yearlings were collected from multiple cohorts (2008–2015), and analyses of their otoliths demonstrated that otolith chemical signatures within hatcheries were consistent between years. Individuals from the Pennsylvania hatcheries were eventually pooled because similarities in the otolith chemical signature of each hatchery made discrimination difficult. Additional details on the pooling of individuals from the Pennsylvania hatcheries are provided by Boehler et al. (2012).

Wild juvenile steelhead were also collected from two Lake Erie tributaries where natural recruitment occurs. In Cattaraugus Creek, New York, wild yearlings were collected with the assistance of the New York State Department of Environmental Conservation (NYSDEC) in July 2009. Fish were also collected in August 2010 from the Grand River, Ontario, by the Ontario Ministry of Natural Resources (OMNR). These fish were interpreted to be resident Rainbow Trout (nonmigratory) because they had typical stream Rainbow Trout coloration and were larger than yearling steelhead collected from other systems in Lake Erie (TL [mean ± SE] = 194 ± 6 mm; range = 150–292 mm). Regardless of whether they were resident or migratory, they provided an accurate otolith chemical signature for the Grand River.

Adult steelhead were collected in conjunction with the Michigan Department of Natural Resources (MDNR), the Ohio Department of Natural Resources (ODNR), the Pennsylvania Fish and Boat Commission (PFBC), and the NYSDEC during fall 2009 and spring 2010. An attempt was made to collect steelhead throughout the fall (late October to early December) and spring (late March to early May) spawning runs to account for seasonal variability in hatchery straying. Fish were collected by use of electrofishing (boat and backpack). Individuals were obtained from five Lake Erie tributaries: the Huron River, Michigan; the Vermilion River, Ohio; Sixteenmile Creek, Pennsylvania; and Chautauqua and Cattaraugus creeks, New York (Figure 2). Collections were obtained near the mouth of each tributary (≤4 km upstream), except in the Huron River, where collections occurred 15 km upstream (Table 1). <AQ: the first call-out of Table 2

preceded the first call-out of Table 1. Therefore, the two tables have been switched (original Table 2 is now Table 1 and vice versa).>

[C]*Five-tributary analysis (2009–2010).*—Once steelhead were collected, their sagittal otoliths were removed by using plastic forceps and were prepared for analysis. Procedures for preparation of otoliths and subsequent chemical analysis have been presented previously (e.g., see Secor et al. 1991; Hayden et al. 2011; Boehler et al. 2012). Briefly, otoliths were cleaned of organic material by sonication in hydrogen peroxide (3% volume/volume) and were air dried. Otoliths were embedded in a two-part epoxy (West System 105 Epoxy Resin and 206 Slow Hardener) and were sectioned in the transverse plane by using a low-speed wafer saw with a diamond-tipped blade. Both sides of the cut otolith cross-sections were wet polished by using Milli-Q ultrapure water with 3M-brand silicon carbide sandpaper and lapping film (particle sizes = 20, 10, 6, and 2 μm) to a thickness of approximately 200 μm. Polished otoliths were mounted on standard petrographic microscope slides by using epoxy. Mounted slides were triple-rinsed and sonicated for 5 min with ultrapure water, were covered and allowed to dry overnight, and then were stored in clean Petri dishes until analyses were performed.

Otoliths were analyzed using laser ablation (LA)–inductively coupled plasma (ICP)–mass spectrometry (MS) at the Great Lakes Institute for Environmental Research (GLIER; University of Windsor, Ontario). A description of LA-ICP-MS and associated operating conditions is presented by Boehler et al. (2012). The theoretical concentration of calcium in stoichiometric calcium carbonate (400,432 μg Ca/g $CaCO_3$) was used as an internal standard to correct for ablation yield differences between external calibration standard and the otoliths, and the occurrence of mass 120 (measured as ^{120}Sn [tin isotope])—an indicator of contamination from the epoxy bonding medium—was also quantified (Ludsin et al. 2006; Reichert et al. 2010). Analysis of a certified standard reference glass (National Institute of Standards and Technology [NIST] 610) was conducted twice, both before and after a group of otoliths (~15) was run, to correct for instrument drift (Elsdon and Gillanders 2006). Although NIST 610 is a glass matrix and not a carbonate matrix like the otoliths, replicate analyses of FEBS-1 (a certified otolith reference material) as an unknown using NIST 610 for calibration with the femtosecond laser system yielded Sr concentrations that were indistinguishable from the accepted values (Hayden et al. 2011; B. Fryer, GLIER, unpublished data). Data processing and calculations of detection limits were performed using a Microsoft Excel spreadsheet macro (Yang 2003) based on algorithms developed by Longerich et al. (1996). In total, 20 isotopes of 15 elements (^{7}Li, ^{25}Mg, ^{33}S, ^{39}K, ^{43}Ca, ^{44}Ca, ^{55}Mn, ^{57}Fe, ^{63}Cu, ^{65}Cu, ^{66}Zn, ^{67}Zn, ^{86}Sr, ^{87}Rb, ^{88}Sr, ^{120}Sn, ^{133}Cs, ^{137}Ba, ^{138}Ba, and ^{208}Pb) were collected, of which only ^{86}Sr and ^{138}Ba (reported as total Sr and Ba) were used for discrimination analysis. Strontium and barium have previously been identified as important discriminators of fish natal origins in the Great Lakes (Brazner et al. 2004; Ludsin et al. 2006; Hand et al. 2008; Pangle et al. 2010; Boehler et al. 2012), and this approach was used because Sr and Ba had concentrations with a lower variance within hatcheries compared to the other elements analyzed. Strontium and barium concentrations were always greater than the limits of detection (Sr [mean ± SE] = 1.24 ± 0.03 µg/g; Ba = 0.044 ± 0.002 µg/g). <AQ: ppm values for Sr and Ba have been changed to micrograms per gram. Please confirm.>

To allow us to identify source-specific otolith chemical signatures and to address variability in steelhead size within hatcheries, otolith regions were standardized using the procedures outlined by Boehler et al. (2012). Briefly, otoliths from steelhead hatchery yearlings were standardized from the core (0%) to the edge (100%), and otoliths from wild stocks (Grand River and Cattaraugus Creek) were standardized from the core (0%) to the first annulus (100%). Average Sr and Ba concentrations were calculated for each 5% otolith increment, but the inner 10% (50–60 µm) of all otoliths was excluded from subsequent analyses to minimize potential maternal influences (Chittaro et al. 2006; Macdonald et al. 2008; Wolff et al. 2012). The remaining 18 Sr variables and 18 Ba variables were entered into a linear discriminant analysis (LDA) and were systematically removed with backward stepwise variable selection until the combination of variables yielding the lowest number of misclassified fish was obtained. To remove the impacts of multicollinearity, any otolith regions that were continuous and highly correlated (pairwise correlation > 0.70) were pooled (McGarigal et al. 2000). In total, eight otolith region variables (5 Sr variables; 3 Ba variables) were included in the final discriminant analyses (Table 2). Because differences in the crystalline structure (aragonite or vaterite) of otoliths cause variation in otolith elemental signatures, only otoliths that were composed entirely of aragonite were included in all subsequent analyses (Zimmerman and Nielson 2003; Gibson-Reinemer et al. 2009). Vateritic otolith sections were identified based on their characteristically low levels of Sr and high levels of Mg (Gauldie 1996; Melancon et al. 2005; Gibson-Reinemer et al. 2009) and were present in approximately 20% of both juvenile and adult steelhead.

Initially, we attempted to separate all source populations of steelhead in a single LDA; however, due to (1) similar mean Ba concentrations in the outer otolith regions between the Pennsylvania hatcheries and Cattaraugus Creek and (2) heavy weighting of the outer regions when all source populations were included in the analysis (especially the Castalia SFH yearlings), discrimination was relatively poor. Therefore, two LDAs were used to maximize source population identification (Boehler et al. 2012; Curtis et al. 2014). A primary LDA was utilized to discriminate among yearlings from Wolf Lake SFH, Castalia SFH, Salmon River SFH, the Pennsylvania hatcheries pooled, and the Grand River. To maximize discriminating power based on otolith chemical signatures of steelhead from the Pennsylvania hatcheries and those of wild fish from Cattaraugus Creek, a secondary LDA was employed. This secondary analysis excluded all other source populations (Castalia SFH, Wolf Lake SFH, Salmon River SFH, and the Grand River), changing the between-group covariance matrix and subsequent variable weightings. Thus, the overall classification accuracy between the Pennsylvania hatchery and Cattaraugus Creek signatures was improved while including the same Sr and Ba otolith regions used in the primary LDA. Only adult steelhead identified as being of Pennsylvania hatchery origin in the primary LDA were included in the secondary LDA (Pennsylvania and Cattaraugus Creek only).

A multivariate ANOVA (MANOVA) was used to test whether the elemental signatures of steelhead source populations in Lake Erie were significantly different. Likelihood probabilities that all yearlings belonged to their correct origin were calculated by using a jackknife procedure (Thorrold et al. 1998; Wells et al. 2003; Walther and Thorrold 2008) for both the primary LDA and secondary LDA. For a fish to be correctly classified, the probability of belonging to its actual hatchery of origin (*p*-actual) had to be greater than 0.50. We report the mean *p*-actual for source populations, allowing individuals that classified correctly but with lower likelihood (i.e., fish with a *p*-actual of 0.60) to have more influence in the overall mean classification (Boehler et al. 2012). All statistical analyses were conducted using JMP version 12.1.0 (SAS Institute, Inc., Cary, North Carolina).

Unlike the hatchery yearling otoliths, which were partitioned into 5% increments from the core to the true otolith edge, adult steelhead otoliths were analyzed from the core (0%) to the demarcation at stocking (100%). All otolith material that occurred after the shift in otolith chemistry between the known-hatchery or first-year chemical signature and the consistent Lake

Erie signature (or potential stream signature in some instances) was ignored. This allowed the source population of unknown-origin adults to be identified with the LDAs generated from the same otolith regions as juveniles.

After the primary analysis of adult steelhead, adults that were identified as being of Pennsylvania hatchery origin in the first LDA were included in the secondary LDA to differentiate adults of Pennsylvania hatchery origin from those of Cattaraugus Creek origin. Like the yearling steelhead, an adult was required to have a *p*-actual exceeding 0.50 for belonging to one of the known source populations; otherwise, that adult was considered of unknown origin.

We estimated state-straying within each tributary as the percentage of steelhead (hatchery and wild) in the total sample that were identified as strays. Adult steelhead were considered state-strays if they returned to a tributary located in a state or province different than the one in which they were released or spawned (e.g., a Pennsylvania hatchery-origin fish collected in a New York tributary as an adult). As such, the reported straying proportions are conservative, since straying among tributaries within each state could not be identified. In addition, neither wild steelhead collected in their state of origin (i.e., Cattaraugus Creek-origin fish collected in New York) nor steelhead identified as being of unknown origin were considered strays. Differences in state-straying between tributaries and between seasons were assessed statistically by using Pearson's chi-square analysis (Pearson's χ^2). We could not calculate a donor stray rate (i.e., the percentage of a source group that strayed) because we could not account for all adult returns from a given source.

[C]*New York tributary analysis (2015).*—To confirm the consistently high straying proportions in the New York tributaries (see Results) and to identify proportional differences in straying within these tributaries, adult steelhead were collected from Cattaraugus and Chautauqua creeks during fall and spring 2015. Adults were collected by using electrofishing (boat and backpack) and shoreline angling from six different locations: 3, 27, and 59 km upstream from the mouth of Cattaraugus Creek; and <1, 3, and 7 km upstream from the mouth of Chautauqua Creek. These distances represent the near-maximum range of each creek system that can be traversed by adult steelhead. Adults were collected in both spring and fall 2015 from all locations in Chautauqua Creek and from the downstream section of Cattaraugus Creek. Due to logistical constraints, fish from the two upstream locations of Cattaraugus Creek were only collected during fall 2015.

All otoliths were removed and prepared by using the same methods described in the five-tributary analysis. Otoliths were also analyzed using the same methods and settings described by Boehler et al. (2012); however, due to an upgrade in LA-ICP-MS at GLIER, a PhotonMachines 193-nm excimer laser coupled to an Agilent 7900 fast-scanning ICP quadrupole mass spectrometer was used. This upgrade did not influence our results, as the same standard (NIST 610) was used to correct for instrument drift.

After otolith chemistry analysis, the proportion of adults from each stocking source and the proportion of state-strays were determined for each tributary section and each season in both New York tributaries. Differences in state-straying between seasons and between stream sections were analyzed by using Pearson's χ^2.

[A]RESULTS

[B]*Otolith Chemical Signatures*

The otolith chemistry of state hatchery steelhead yearlings (Wolf Lake SFH, Michigan; Castalia SFH, Ohio; Salmon River SFH, New York; and the Pennsylvania hatcheries) along with the Grand River, Ontario, yearlings was found to be significantly different with the primary LDA (overall MANOVA: Wilks' λ, $F_{32,\,629} = 64.25$, $P < 0.0001$). The first two canonical axes (CAs) accounted for 99.6% of the total variance (CA1 = 94.1%, eigenvalue = 30.5; CA2 = 5.5%, eigenvalue = 1.8; see canonical scoring coefficients, Table 3). The mean jackknifed classification accuracy ranged from 72.1% (Wolf Lake SFH) to 100.0% (Castalia SFH). Overall, the primary LDA accurately classified 94.9% (224 of 236) of the juvenile steelhead (Table 4).

Because discrimination between the Pennsylvania hatchery-origin fish and the naturally reproduced steelhead from Cattaraugus Creek, New York, was critical to our conclusions, the secondary LDA was employed to maximize the discrimination of these two source populations (overall MANOVA: Wilks' λ, $F_{8,\,165} = 36.65$, $P < 0.0001$). This secondary LDA utilized the same otolith regions as the primary LDA and also had high mean jackknifed classification accuracies (Pennsylvania hatcheries: 88.6%; Cattaraugus Creek: 90.1%), with 91.4% (159 of 174) of the juvenile steelhead being correctly classified (Table 4). The CA1 explained 100% of the total variance (eigenvalue = 1.8) in the secondary LDA (canonical scoring coefficients, Table 3).

[B]*Five-Tributary Analysis (2009–2010)*

Lake Erie tributaries had state-straying instances of 88% (Cattaraugus Creek, New York), 72% (Chautauqua Creek, New York), 57% (Huron River, Michigan), 23% (Sixteenmile Creek, Pennsylvania), and 18% (Vermilion River, Ohio; fall and spring combined; Table 5). The proportion of state-strays for each tributary was similar in both fall and spring sampling periods (Pearson's χ^2: all $P > 0.05$), except in the Vermilion River, where significantly more state-strays were identified during fall (Pearson's χ^2: $P = 0.0124$). Most of the state-strays were Grand River-origin steelhead in the Huron River; New York hatchery-origin fish in Sixteenmile Creek; and Pennsylvania hatchery-origin fish in the Vermilion River, Cattaraugus Creek, and Chautauqua Creek. All Lake Erie tributaries contained strays from multiple sources (range = 2–4 sources), and unknown-origin individuals were identified in Cattaraugus, Chautauqua, and Sixteenmile creeks.

In the two New York tributaries, Pennsylvania hatchery-origin individuals made up the greatest proportion of fish identified (Chautauqua Creek: fall 67%, spring 29%; Cattaraugus Creek: fall 60%, spring 43%) except in the spring Chautauqua Creek collections, when a higher proportion of Ohio hatchery-origin fish were captured (39%). The proportions of Pennsylvania hatchery-origin fish were significantly lower during spring collection periods (Pearson's χ^2: both $P < 0.0147$); during both spring periods, the decrease in Pennsylvania hatchery-origin fish coincided with a proportional increase in Ohio hatchery-origin fish (Chautauqua Creek: 34% increase; Cattaraugus Creek: 9% increase).

Wild fish made up 9% of the steelhead catch in Lake Erie tributaries during the 2009–2010 study period (Table 5). Wild Cattaraugus Creek-origin steelhead were identified in Sixteenmile Creek (1.6% of the total catch) along with Chautauqua and Cattaraugus creeks (4.5% and 2.7% of the total catch, respectively). Grand River-origin fish were identified in each tributary sampled except Chautauqua Creek (Huron River: 43.2% of the total catch; Vermilion River: 2.1%; Sixteenmile Creek: 3.2%; Chautauqua Creek: 0.0%; Cattaraugus Creek: 2.7%).

[B]*New York Tributary Analysis (2015)*

The proportions of state-strays identified in Cattaraugus (80%) and Chautauqua (84%) creeks at the locations closest to the mouth were like those observed in 2009–2010 (Pearson's χ^2, spring and fall combined: both comparisons $P > 0.1423$). Overall, 74% of all individuals captured in Cattaraugus Creek and 68% of all individuals captured in Chautauqua Creek were state-strays (spring and fall combined; Table 6). In both seasons, the proportions of state-strays were similar in all stream sections of Cattaraugus Creek (Pearson's χ^2: all comparisons $P > 0.05$); in Chautauqua Creek, only the proportion of state-strays found in the section closest to the mouth (<1 km) was significantly greater than that observed in the tributary section furthest upstream (7 km; Pearson's χ^2 comparison of <1- and 7-km sites, fall: $P = 0.0308$, spring: $P = 0.0201$; all other comparisons $P > 0.05$). In comparisons of fall and spring sampling periods, the proportions of state-strays were similar in all stream sections (Pearson's χ^2: all comparisons $P > 0.05$), but seasonal comparisons could not be made for the two upstream sections of Cattaraugus Creek, as no fish were collected during spring sampling (Table 6).

In 2015, Pennsylvania hatchery-origin fish made up half of the total number of individuals collected in Chautauqua Creek, followed by New York hatchery-origin (21%), Ohio hatchery-origin (12%), wild New York-origin (11%), Michigan hatchery-origin (5%), and wild Ontario-origin (1%) fish. Like Chautauqua Creek, collections in Cattaraugus Creek consisted mostly of Pennsylvania hatchery-origin steelhead (57%). Wild Cattaraugus Creek individuals were the next most common (17%), followed by New York hatchery-origin fish (10%) and Michigan and Ohio hatchery-origin fish (8% each). The proportion of Pennsylvania hatchery-origin fish identified was significantly lower in spring than in fall (Pearson's χ^2: $P = 0.006$). Conversely, the proportion of Ohio hatchery-origin fish identified was higher during the spring season (Pearson's χ^2: $P < 0.001$). The percentage of New York hatchery-origin fish was higher in spring than in fall (Pearson's χ^2: $P = 0.034$), and no proportional difference was identified for wild Cattaraugus Creek individuals among seasons (Table 6).

The proportion of Michigan hatchery-origin steelhead found in each section of the New York tributaries varied (range = 0–20%). Michigan hatchery individuals were identified in each section of both tributaries and during most sampling periods. Throughout 2015 sampling, only one wild Ontario individual was identified, and that fish was found in the downstream section of Cattaraugus Creek (Table 6).

[A]DISCUSSION

Hatchery-stocked individuals and wild steelhead from New York and Ontario were clearly discriminated based on elemental signatures from otolith transects. The high jackknifed classification accuracies and low numbers of misclassified fish in the LDAs without removal of statistical outliers suggested that analyses were robust and not limited by sample size (McGarigal et al. 2000). The LDAs generated here could be used for future studies if the ambient water chemistry in hatcheries (or in natal tributaries) remains constant among years.

The percentages of state-stray steelhead in New York tributaries were higher (72–88% of the total catch) than percentages in the other Lake Erie tributaries we sampled (18–57% of the total catch). The use of state-straying values should be considered conservative because we identified hatchery stocking source by state and not by the specific tributary of stocking. In the Vermilion River, state-strays were mostly of Pennsylvania hatchery origin, whereas in Sixteenmile Creek, most state-strays were of New York hatchery origin. This may represent a preference by steelhead to stray to geographically proximate locations rather than to travel longer distances—a tendency that has been identified previously in straying steelhead (Lirette and Hooton 1988; Schroeder et al. 2001; Brenner et al. 2012). In the Huron River, 43% of the adult steelhead collected were identified as being of Grand River origin. Although the jackknifed classification accuracy for Grand River juveniles was high (91%), we cannot be certain that many of the adult steelhead classified as Grand River origin did not originate from other sources for which we did not have otolith chemistry data. For example, both the Grand River and the southeastern shoreline of Lake Huron share the same geological terrane (Marklevitz et al. 2011), potentially making the otolith chemical signatures of steelhead originating from this region difficult to discriminate from the Grand River signature. The possibility that Lake Huron-origin steelhead were misclassified is also feasible considering the connectivity that exists between Lake Huron and Lake Erie waters and the high proportion of adult steelhead captured in the Huron River that were predicted to be wild individuals of Grand River origin.

The adult steelhead in Cattaraugus and Chautauqua creeks were overwhelmingly of Pennsylvania hatchery origin (52% of the total New York catch) and Ohio hatchery origin (17% of the total New York catch). Stocking practices and their relationship with stream imprinting may play a substantive role in the high proportion of strays found in New York streams, as both Pennsylvania and Ohio stocking programs implement near-mouth releases. For example, the state of Ohio annually stocks approximately 60,000 steelhead yearlings into the Vermilion River within 2 km from Lake Erie. Similarly, the state of Pennsylvania stocks approximately 111,000 steelhead yearlings into Twentymile Creek within 1 km from the lake. A short emigration distance may result in poor stream imprinting for these fish, especially during years when high tributary flow rates result in rapid emigration (Melnychuk et al. 2010). The number of juvenile steelhead present in Pennsylvania and Ohio tributaries could also contribute to increased straying potential, as high densities of smolts can promote rapid emigration from these systems (Keeley 2001).

In addition to rapid emigration after stocking, the large number of juvenile steelhead stocked by both Pennsylvania and Ohio hatcheries may alone contribute to the large percentage of individuals from these stocking programs captured in New York tributaries. Pennsylvania stocks approximately 1.1 million steelhead yearlings annually into 13 Lake Erie tributaries, and Ohio stocks approximately 420,000 yearlings into five tributaries. In their review of the literature on straying, Keefer and Caudill (2014) reported mean donor straying to be 13.8% in steelhead. Based on this rate, the donor population of hatchery strays would be 151,800 from Pennsylvania hatcheries and 62,100 from Ohio hatcheries, assuming that all fish survive and spawn. Because steelhead have a propensity to stray to geographically proximate locations (Lirette and Hooton 1988; Schroeder et al. 2001), many of these individuals would be expected to stray to New York tributaries, potentially contributing to the increased proportion of strays present. Many studies have reported an exponential increase in the number of straying salmonids with decreasing distance from a release site (Quinn and Fresh 1984; Unwin and Quinn 1993; Candy and Beacham 2000; Thedinga et al. 2000; Bartron et al. 2004; Correa and Gross 2008; Brenner et al. 2012; Westley et al. 2013); consequently, the closer proximity of Pennsylvania stocking locations to New York tributaries, along with the greater number of fish stocked, likely explains the larger proportions of Pennsylvania hatchery-origin strays identified in New York tributaries compared to strays identified from Ohio hatcheries (Pennsylvania: 57%; Ohio: 17%). Twentymile Creek, Pennsylvania, which is stocked with over 44% of the entire New York annual stocking program for Lake Erie (~111,000 hatchery fish), would be expected to provide the greatest contribution of hatchery strays to New York tributaries, as it is less than 17 km from the mouth of Chautauqua Creek and less than 63 km from the mouth of Cattaraugus Creek. In fact, NYSDEC biologists (J. Markham, NYSDEC, Lake Erie Fisheries Unit, Dunkirk, personal communication) have found yearling steelhead of stocking size in lower Chautauqua Creek during spring before they stock fish (i.e., Pennsylvania stocks up to 1 month earlier than New York), suggesting that fish stocked by other state hatchery systems exhibit exploratory behavior to New York tributaries even before completely transitioning to the lake phase of their life cycle.

State-straying percentages could also be exacerbated in New York tributaries by poor returns of New York hatchery fish. The Salmon River SFH yearlings released into New York tributaries are stocked at less than 150 mm on average (mean TL ranges from 114 to 137 mm; J. Markham, NYSDEC, Lake Erie Fisheries Unit, personal communication), which is below the approximate size threshold for juvenile steelhead emigration (Wagner et al. 1963; Seelbach 1987; Peven et al. 1994; Quinn 2005). If Salmon River SFH yearlings are too small to physiologically smolt and are not ready to emigrate, then their longer residency may lead to substantive instream mortality because of high summer temperatures, predation, and competition with wild yearlings (Wagner 1968; Keeley 2001; Hill et al. 2006). Slaney et al. (1993) reported a threefold increase in survival for steelhead smolts stocked at 180 mm compared to those stocked at 145 mm. Thus, poor contribution of the Salmon River SFH stock to New York streams may contribute to the higher-than-expected proportion of Pennsylvania and Ohio hatchery-origin steelhead in New York tributaries.

The identification of wild-origin adult steelhead in Lake Erie tributaries (15% of the total catch) suggests that naturally reproduced individuals are contributing to the fishery. This moderate natural reproduction is another potential driver of the large proportion of Pennsylvania and Ohio strays identified in New York tributaries. Abundant juvenile steelhead have been identified in some main-stem tributaries of New York streams (NYSDEC 2006), and it is possible that odors from naturally reproduced fish attract adult steelhead from other systems. Unlike most Lake Erie tributaries that support very little successful reproduction due to high summer temperatures (Thompson and Ferreri 2002), Chautauqua and Cattaraugus creeks support steelhead year-round (Goehle 1999), potentially allowing continuous odor marking of stream substrate to occur. Atlantic Salmon *Salmo salar* parr can recognize conspecific pheromones deposited in stream substrates (Stabell 1987), but the concentration of the odor also influences whether a preference is observed (Courtenay et al. 2001). Even though adult salmonids can also discriminate between populations (Stabell 1992; Brown and Brown 1996), the role played by chemical odors (i.e., pheromones) in homing is still uncertain (Quinn 2005; Ueda 2012).

We found no evidence that state-straying individuals were more likely to travel further upstream to find suitable spawning sites. Little difference in state-straying proportions was identified in each section of Cattaraugus and Chautauqua creeks, indicating that straying individuals utilized both upstream and downstream sections of these tributaries. *Oncorhynchus* species commonly home non-directly to two or more alternate sites before reaching their final spawning destination, but this non-direct homing is confined to the lower reaches of nearby tributaries (Burger et al. 1995; Keefer et al. 2008). The similar proportions of strays identified in the lower, middle, and upper reaches of the New York tributaries suggest that these individuals are in fact strays rather than individuals utilizing additional tributaries on their way to their final spawning site.

At all tributary locations, the proportions of Pennsylvania hatchery-origin fish identified in Chautauqua Creek were lower during spring sampling periods than during fall sampling periods. It is unclear whether the reduction in the proportion of Pennsylvania hatchery-origin fish during the spring season is the result fewer Pennsylvania hatchery-origin individuals straying into New York tributaries, an increase in Ohio hatchery-origin fish straying in the spring, or some combination of the two. Each year, the state of Pennsylvania performs six adult steelhead collections from November to February to obtain broodstock for the hatchery program (Vargason 2013). Because spring sampling occurred in April, it is possible that many of the Lake Erie-strain steelhead stocked by Pennsylvania had already spawned and left the New York tributaries before the sampling occurred. Conversely, peak spawning of Manistee-strain steelhead stocked by the state of Ohio occurs in March–April (Seelbach 1993; Seelbach et al. 1994) and may be responsible for the increased number of Ohio strays present in Cattaraugus and Chautauqua creeks during spring sampling periods.

In summary, our results provide state fishery managers with new and valuable information regarding the presence of state-straying adult steelhead in Lake Erie tributaries. Future otolith chemistry studies, including assessments of source populations from multiple Great Lakes, could greatly increase the knowledge gained about steelhead movement within and between systems (Landsman et al. 2011). For example, Barnett-Johnson et al. (2010) found that coupling otolith chemistry with genetic analysis further increased stock resolution. There is also a need to quantify run numbers into Lake Erie tributaries so that straying rates and total numbers of strays can be determined. Although straying rates could not be evaluated here, high proportions of steelhead from Ohio and Pennsylvania state hatcheries were present in the Lake Erie tributaries of New York. Strategies to reduce straying may include practicing upstream stocking, reducing the number of individuals stocked, and fostering management decisions that improve spawning and nursery habitat.

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TABLE 1.—Timing of collection and characteristics of adult steelhead from Lake Erie tributaries.

Year(s)	Tributary	Dates sampled (fall, spring)	*N* (fall, spring)	Average TL (mm; ±SE)	Upstre distance
2009–2010	Huron River, Michigan	Dec 1, Apr 20	33, 11	595 ± 12.9	15
	Vermilion River, Ohio	Nov 23, Apr 13	49, 47	576 ± 11.0	4
	Sixteenmile Creek, Pennsylvania	Nov 17, March 10	41, 21	563 ± 10.8	<1
	Chautauqua Creek, New York	Oct 30, Apr 15	39, 28	534 ± 13.9	<1
	Cattaraugus Creek, New York	Oct 19, Apr 13	40, 34	505 ± 13.1	3
2015	Chautauqua Creek	Oct 26–Nov 17, Apr 15–May 5	68, 44	567 ± 6.7	<1, 3
	Cattaraugus Creek	Nov 4–18, Apr 30–May 5	62, 10	529 ± 10.0	3, 27,

TABLE 2.—Description of yearling steelhead that were included in discriminant analyses (SFH = State Fish Hatchery). Also listed are average concentrations (µg/g [mean ± SE]) of Sr and Ba for each otolith region used.

				Element, otolith			
Juvenile steelhead source	Year	*N*	Average TL (mm; ±SE)	Sr, 80–95%	Sr, 55–60%	Sr, 45–50%	3

				Element, otolith			
Wolf Lake SFH, Michigan	2008, 2009, 2015	10, 14, 11	185 ± 2.9	436 ± 13	412 ± 13	403 ± 15	42
Salmon River SFH, New York	2008, 2010, 2015	16, 10, 9	122 ± 2.8	253 ± 6	333 ± 17	387 ± 22	38
Castalia SFH, Ohio	2009, 2015	16, 13	153 ± 3.3	1,563 ± 40	1,106 ± 106	1,158 ± 124	1,2
Pennsylvania hatcheries pooled	2008, 2009, 2015	44, 48, 21	168 ± 1.7	319 ± 7	338 ± 7	339 ± 7	3
Grand River, Ontario	2010	24	194 ± 6.0	597 ± 10	528 ± 13	537 ± 13	58
Cattaraugus Creek, New York	2009	61	130 ± 2.9	220 ± 6	218 ± 8	203 ± 6	1

TABLE 3.—Canonical scoring coefficients for the primary linear discriminant analysis (LDA; all steelhead groups except Cattaraugus Creek, New York) and secondary LDA (Pennsylvania hatcheries and Cattaraugus Creek only) on elemental concentrations of yearling steelhead.

	Element, otolith region (percent distance from the core)							
Canonical axis (CA)	Sr, 80–95%	Sr, 55–60%	Sr, 45–50%	Sr, 35–40%	Sr, 10–15%	Ba, 80–85%	Ba, 45–50%	E 10–
				Primary LDA				
CA1	0.01238	–0.00314	0.00137	0.00048	0.00225	–0.06474	–0.06111	–0.0
CA2	0.00213	–0.00090	–0.00358	0.00341	0.00137	0.04650	0.16888	0.05
				Secondary LDA				

Canonical axis (CA)	Element, otolith region (percent distance from the core)							
	Sr, 80–95%	Sr, 55–60%	Sr, 45–50%	Sr, 35–40%	Sr, 10–15%	Ba, 80–85%	Ba, 45–50%	B 10–
CA1	0.00531	0.00226	0.00460	0.00731	0.00081	–0.00968	–0.08514	0.03

TABLE 4.—Jackknifed classification accuracy for primary and secondary linear discriminant analyses (LDAs) of yearling steelhead. Fish with a *p*-actual greater than 0.50 were designated as having been correctly classified (groups: MI = Wolf Lake State Fish Hatchery [SFH], Michigan; NY = Salmon River SFH, New York; OH = Castalia SFH, Ohio; WON = wild Ontario fish; PA = Pennsylvania hatcheries pooled; WNY = wild New York fish).

LDA (jackknifed)	Primary LDA					Secondary LDA	
	MI	NY	OH	WON	PA	WNY	PA
Classification accuracy (%; mean *p*-actual)	72.1	86.1	100.0	90.6	88.7	90.1	88.
Range (%; *p*-actual)	13.8–95.3	52.5–97.3	100.0–100.0	48.3–99.9	0.14–100.0	1.2–99.9	0.0–9
Number misclassified	4	0	0	1	7	5	10
Total *N*	35	35	29	24	113	61	113

TABLE 5.—Number and predicted origin of adult steelhead captured in five Lake Erie tributaries during fall 2009 and spring 2010 (hatchery groups: Wolf Lake State Fish Hatchery [SFH], Michigan; Castalia SFH, Ohio; Pennsylvania [PA] hatcheries pooled [see Methods]; and Salmon River SFH, New York). Numbers of non-straying fish are indicated in bold italics. Fish of unknown origin were not considered strays.

		Predicted hatchery origin				Predicted v
Tributary sampled	Season	Wolf Lake SFH	Castalia SFH	PA hatcheries (pooled)	Salmon River SFH	Cattaraugus Creek, New York
Huron River, Michigan	Fall	***14***	5			
	Spring	***5***			1	
	Total	***19***	5		1	
Vermilion River, Ohio	Fall	1	***45***	2	1	
	Spring	2	***34***	9		
	Total	3	***79***	11	1	
Sixteenmile Creek, Pennsylvania	Fall	1		***31***	7	1
	Spring			***15***	3	
	Total	1		***46***	10	1
Chautauqua Creek, New York	Fall	1	2	26	***9***	***1***
	Spring		11	8	***6***	***2***
	Total	1	13	34	***15***	***3***
Cattaraugus Creek, New York	Fall	1	10	24	***2***	***1***
	Spring	2	12	15	***2***	
	Total	3	22	39	***4***	***1***

TABLE 6.—Number and predicted origin of adult steelhead captured in New York tributaries at different upstream locations in spring and fall 2015 (hatchery groups: Wolf Lake State Fish Hatchery [SFH], Michigan; Castalia SFH, Ohio; Pennsylvania [PA] hatcheries pooled [see Methods]; and Salmon River SFH, New York). Numbers of nonstraying fish are indicated in bold italics.

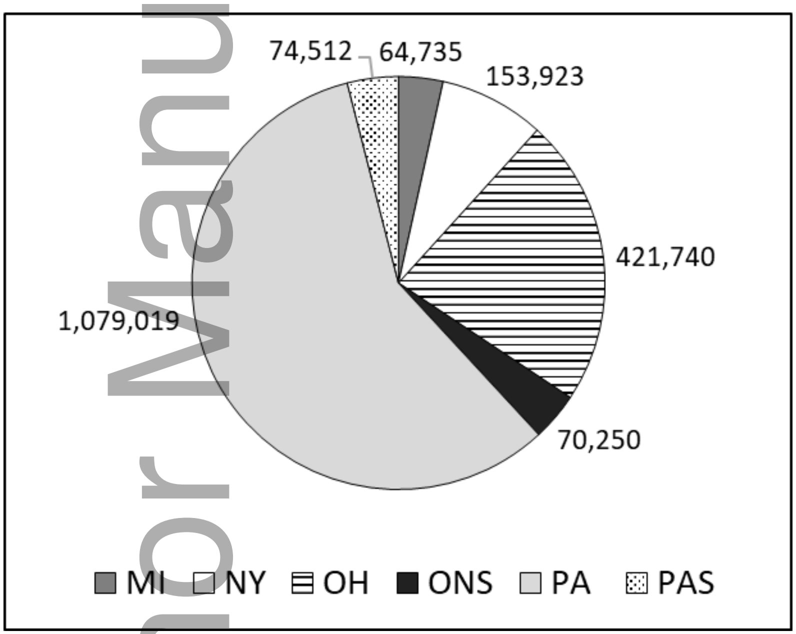
			Predicted hatchery origin			
Tributary sampled	Collection site (km from mouth)	Season	Wolf Lake SFH	Castalia SFH	PA hatcheries (pooled)	Salmon Rive SFH
Chautauqua Creek, New York	1 (<1)	Spring	2	2	7	***2***
		Fall	1		18	***4***
		Total	3	2	25	***6***
	2 (3)	Spring	1	7	3	***3***
		Fall		1	12	***1***
		Total	1	8	15	***4***
	3 (7)	Spring		3	4	***8***
		Fall	2		12	***6***
		Total	2	3	16	***14***
Cattaraugus Creek, New York	1 (3)	Spring	2		6	***1***
		Fall	1	6	13	***2***
		Total	3	6	19	***3***
	2 (27)	Fall	2		10	***3***
	3 (59)	Fall	1		12	***1***

FIGURE 1.—Pie chart depicting the number of juvenile steelhead that were stocked into Lake Erie bays and tributaries by state fishery management agencies and sportsmen's organizations in 2015 (MI = Michigan Department of Natural Resources; NY = New York State Department of Environmental Conservation; OH = Ohio Division of Wildlife; PA = Pennsylvania Fish and Boat

Commission; PAS = Pennsylvania sportsmen's organizations; ONS = Ontario sportsmen's organizations). Data are from the 2015 report of the Lake Erie Coldwater Task Group (CWTG 2016).

FIGURE 2.—Locations of state hatcheries where yearling steelhead were collected and locations of Lake Erie tributaries where adult steelhead were collected (COH = Castalia State Fish Hatchery [SFH], Ohio; LPA = Linesville SFH, Pennsylvania; TPA = Tionesta SFH, Pennsylvania; FPA = Fairview SFH, Pennsylvania; 3PA = 3-C-U Trout Association's Erie County Cooperative Trout Nursery [private hatchery], Pennsylvania). Not included on the map are Wolf Lake SFH (Michigan) and Salmon River SFH (New York), both of which are over 200 km from Lake Erie.

Budnik Figure 1.



Budnik Figure 2.