Chemical tracking of northern pike migrations: If we restore access to breeding habitat, will they come?

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ABSTRACT

Landscape alterations can obstruct movement corridors and degrade spawning habitats for migratory fishes, requiring expensive restoration efforts. To assess use of natural and artificial waterways for spawning migrations, we monitored adult migrations and young-of-year production of northern pike (*Esox lucius*) for two years in six adjacent tributaries of southern Green Bay on Lake Michigan, USA. Field observations were compared with natal origins of young-of-year and adults inferred from otolith microchemistry. Individual tributaries varied widely in their production of young-of-year pike. Microchemical differences were apparent only among tributaries whose watersheds differ in land use, and adult pike showed no evidence of homing even to the same tributary land use class where they were born. Though otolith microchemistry suggests a lack of fidelity to natal streams, carbon stable isotope ratios of adult pike showed a latitudinal gradient across tributaries, suggesting that adult pike do not mix freely outside of the breeding season. Both field observations and microchemical tracing suggest that pike can potentially recolonize historical or newly-created breeding habitats after restoration efforts make them accessible.

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Introduction

Migratory fish rely on moving among multiple habitats to complete their life cycle, making them vulnerable to habitat degradation and fragmentation. For a population to persist, migratory corridors must connect the habitats used for spawning with suitable areas for feeding and seasonal refuges. Conversion of natural landscapes into agricultural and urban land use can degrade aquatic habitats, thereby negatively impacting fish populations (Allan, 2004; Danz et al., 2007). Land development also causes the construction of dams (Esselman et al., 2011) and road crossings (Januchowski-Hartley et al., 2013) which can reduce habitat connectivity and limit dispersal for migratory species (Freeman et al., 2003). At the same time, these land use changes can create novel stream conditions such as ephemeral flow or drainage channels where no stream existed before. Conservation efforts are increasingly addressing the effects of these habitat alterations, including removal of dams and perched culverts, to restore access to spawning habitat for migratory fishes.

Migratory species that exhibit natal homing behavior are particularly susceptible to loss of breeding habitat because individual fish strongly prefer to spawn only in their natal location (Keefer et al., 2008; McIntyre

et al., in press). Restoration efforts can account for this philopatry by reestablishing habitat connectivity and then seeding restored spawning habitats with young fish that can imprint there, thereby renewing the population that will home to the restored area upon adulthood (Gorsky et al., 2009). Alternatively, for species that undergo spawning migrations without natal homing, restored access to breeding habitats may be discovered and utilized without further intervention. Thus, determining the homing tendencies of migratory fish species is essential for managing their populations and maximizing benefits from habitat restoration.

In the Great Lakes of North America, many species of fishes migrate into tributaries to reproduce. Economically- or ecologically-important native species have been the subject of tracking studies to better understand the habitat needs of both adults and larvae in hopes of enhancing population sizes (Landsman et al., 2011). Tracking studies have also attempted to assess the homing tendencies of migratory species. For example, lake trout, *Salvelinus namaycush* (Negus, 2010) and walleye, *Sander vitreus* (Stepien et al., 2009) show spawning site fidelity while sea lamprey, *Petromyzon marinus* (Bergstedt and Seelye, 1995) do not. The majority of fish movement studies within the Great Lakes have used traditional tracking techniques with artificial tags (Landsman et al., 2011). While artificial tags provide important information about movement of large fishes, they are not applicable to larval fishes, and thus can shed little light on natal homing tendencies. Otolith microchemistry offers an alternative, natural tracer that is accreted

throughout a fish's life, and thus is well suited for studies of larval sources and natal homing (Landsman et al., 2011; Pracheil et al., 2014). Daily growth and environmental chemistry inferred from otoliths can be used together to reconstruct spatial and temporal patterns of performance and movement of an individual fish throughout its life (Elsdon et al., 2008). Fishery management decisions are increasingly informed by insights from otolith chemistry into habitat use and stock identification across a variety of spatial scales (e.g. Hand et al., 2008; Pangle et al., 2010; Reichert et al., 2010). For example, otoliths collected from YOY born in different habitats can be used to map chemical variation across a region (Pangle et al., 2010), enabling subsequent assessment of the homing tendencies of breeding adults by comparing their natal chemistry to that of YOY collected at the same location (Engstedt et al., 2014).

Though more often used for food web analysis, stable isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) in fish muscle can also be used to assess spatial ecology of fishes (e.g., Hoffman et al., 2012; Jepsen and Winemiller, 2007). Unlike otolith chemistry, muscle isotope signatures from early life history are diluted away by later growth (Herzka and Holt, 1999). Thus, analysis of muscle from adults cannot address natal origins, but does provide an independent tracer of habitat use during the months prior to sampling (Heady and Moore, 2013; McIntyre and Flecker, 2006) that offers insights into the spatial population structure (Layman, 2007; Reimchen et al., 2008) on ecological time scales that may not be reflected by genetic methods (Pracheil et al., 2014).

Information derived from chemical analysis of otoliths and muscle tissue can be combined to inform restoration efforts for fish populations (Pracheil et al., 2014). For example, otoliths collected from YOY born in different habitats can be used to map chemical variation across the study region (Pangle et al., 2010), and in turn, homing tendencies of breeding adults can be tested by comparing their natal chemistry to that of YOY collected at the same location (Engstedt et al., 2014). If breeding sites can be distinguished reliably using chemical analyses, managers could refine restoration efforts by focusing on the breeding areas that contribute most to recruitment. This approach may be particularly applicable to migratory species for which natal homing tendencies of adults could determine whether restored breeding habitats must be seeded with young fish in order to allow imprinting and subsequent use for spawning. In parallel, muscle isotopes can be used to assess whether adults that migrate to breed in different locations represent spatially distinct population segments, thereby elucidating the need to manage the species as multiple distinct stocks.

Northern pike, *Esox lucius*, are an ideal model species to help resolve restoration needs for migratory fishes. Pike are top predators in shallow habitats of lakes and rivers, but often migrate into tributary streams to breed. In the Great Lakes, boosting northern pike populations is a current management objective (Wisconsin's Changing Climate: Impacts and Adaptation, 2011), but the relative importance of specific breeding locations in order to maintain the population as a whole has received little attention (Landsman et al., 2011). Clark (1990) observed a high recapture rate and overall sedentary behavior of northern pike (*E. lucius*), and inferred this as possible evidence of homing in Lake Erie. In the Baltic Sea, Engstedt et al. (2014) recently reported strong evidence of natal homing in anadromous northern pike based on otolith microchemistry. Resolving the natal homing tendencies of northern pike in the Great Lakes can elucidate whether populations will be enhanced more by improving habitat in existing spawning sites or restoring access to historical breeding habitats.

In this study, we combine field observations, otolith chemistry data, and muscle stable isotope data to assess recruitment and habitat use of northern pike in six adjacent tributaries of southern Green Bay, Lake Michigan. Specifically, we use: 1) field observations to assess spatial distribution of adult breeding activity and subsequent YOY production across a variety of tributary and land use classes, 2) otolith chemistry to chemically map adult breeding grounds based on known-origin YOY, enabling inferences about natal homing by adult northern pike,

and 3) stable isotopes of C and N in muscle of adults to infer their recent habitat use. Our overarching interest is the relative contribution of different tributary classes to northern pike recruitment, and the implications of these spatial patterns for the effectiveness of restoring breeding habitats and river connectivity for pike and other migratory fishes.

Methods

Study region

Northern pike in the Great Lakes often breed in tributaries where floodplains and wetlands provide spawning habitats with submerged vegetation. The region has undergone significant wetland conversion (e.g. Michigan and Wisconsin have converted 25% (Herbert et al., 2010) and 46% (Dahl, 1990) respectively, of their total wetland area since 1850), which may limit breeding habitat choices for pike. We studied six adjacent watersheds along the southwestern shore of Green Bay, Wisconsin, encompassing four natural rivers (Duck Creek, Suamico River, Little Suamico River, Pensaukee River) and two man-made drainage ditches (Lineville Road Ditch, Brown Road Ditch) that collectively drain approximately 1270 km² along 57 km of coastline (USEPA, 2011). Less than seven percent of the study area is wetlands, while over sixty-six percent has been converted for agricultural purposes, including enhancing drainage by creating ditches (Herbert et al., 2010; USEPA, 2011). Even though Green Bay is a highly-altered ecosystem, it still supports a substantial recreational fishery for northern pike (Brazner, 1997). Migrating pike spawn in both the natural tributaries and drainage ditches in our study area, but the relative number of spawning adults and subsequent recruits in each watershed are unknown.

These six basins represent a latitudinal land use gradient from agricultural (north) to increasingly urban (south) (Fig. 1). The ditches have been the focus of recent habitat restoration efforts that have constructed wetland scrapes, planted aquatic vegetation as spawning substrate for pike, and enhanced connectivity via culvert replacements (Paoli, 2012). There are over 1000 road-stream crossings across the study region, of which approximately 30% are at least partial barriers to fish migrations (Januchowski-Hartley et al., 2014). The only two mainstem dams in the study area occur in close succession on Duck Creek a few kilometers upstream of Green Bay; they make the middle and upper reaches inaccessible to pike.

We sampled a total of ten sites in the six focal basins. For statistical analyses, we compared otolith chemistry data at three hierarchical levels of spatial grouping: individual sub-basins (n = 10), focal basins (pooling sub-basins within basins; n = 6), and tributary classes (pooling basins by land use; n = 3). Focal basins were grouped into tributary classes based on similarities in land use and geology, both of which could affect otolith chemistry or pike recruitment potential. The three northern basins (Suamico, Little Suamico, and Pensaukee Rivers; two, two, and three sampling sites, respectively), form one group which is characterized by heavy agricultural use (56–67%), low urban development (<9%), and surficial geology dominated by clay and silt in the lower reaches of the tributary networks with loamy-till moraine and gravel deposits in the headwaters (hereafter referred to as the agricultural tributary class). A second group consists of the two man-made ditch drainages (Brown and Lineville Roads, each with one sampling site) characterized as channelized, ephemeral streams with small catchment area draining only clay and silt deposits near the shoreline of Green Bay (hereafter ditch tributary class). Duck Creek was alone in the third group; its lower reaches are dominated by urban land use (up to 69% in reaches below the dams; 17% across the whole watershed) and drain clay and silt deposits (hereafter referred to as urban tributary class). In Duck Creek, lack of access to upstream habitats limited adult spawning to two areas below the dams, but only one of these produced YOY to qualify as a sampling site. We summarized land use, surficial
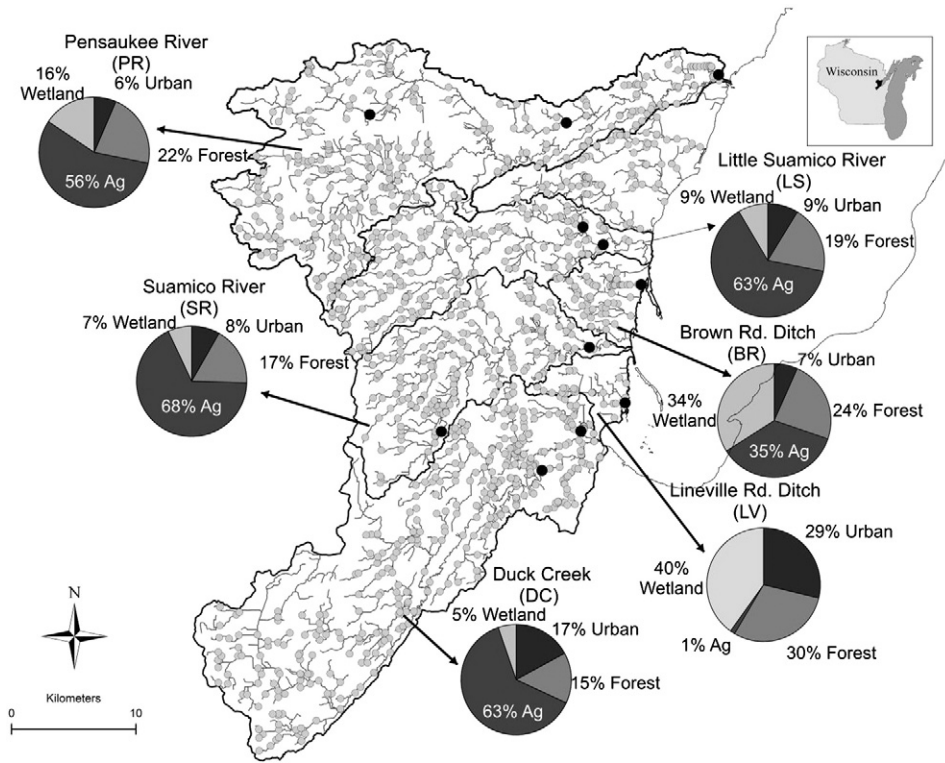
Fig. 1. Map of the Green Bay study region including catchment boundaries for each focal basin (bold lines), land use statistics (pie charts), road crossings (gray circles), and fish sampling locations (black circles).
Data compiled from USEPA and USGS, 2005; Fry et al., 2011.

geology, and road crossings for all study basins using regional datasets using ArcMap 10.1 (Fig. 1, Electronic Supplementary Material (ESM) Table S1).

Field surveys and otolith collections

To assess spatial and temporal distributions of adult breeding activity and young-of-year (YOY) production, we systematically searched for spawning adults and monitored YOY production from the six focal basins throughout the entire spawning and YOY emigration period of 2011 and 2012 (Table 1). Our assessment encompassed both extremes of stream hydrology for the study region; 2011 had an unusually wet spring; whereas, 2012 had an unusually dry spring (USGS,

2013, Fig. S1). We systemically searched for spawning pike that migrated greater than 0.5 km inland from Green Bay into each basin. These surveys of adults were used to identify migration corridors and spawning locations within each watershed, but we did not attempt to quantify every breeder in each site. Most of the places we surveyed represent sites (sometimes ephemeral) which rapidly warm or desiccate in mid-summer, thereby excluding the possibility of a resident pike population (YOY or adult). Our final sampling locations represented discrete tributaries into which adults had to choose to migrate, and YOY had no choice but to drift downstream back towards Green Bay. Our ten sampling sites include a variety of habitats with substantial breeding activity, but no quantitative assessment of adult densities was possible given the size of the study area and short duration of spawning activity. All

Table 1
Summary statistics for otolith collections, breeding surveys, and YOY production for focal basins, their sub-basins, and voucher adult pike specimens.

Tributary class	Basin	Sub-basin	Adult otoliths 2011	Adult otoliths 2012	Adult breeders 2011	Adult breeders 2012	YOY otoliths 2011	YOY otoliths 2012	YOY recruits 2011	YOY recruits 2012
Ditch	Brown Road	Brown Road	5	4	30	30	3	49	132	10
Urban	Duck Creek	Brookfield	12	8	24	13	8	2	13	3
		Pamperin Park	17	0	36	15	0	0	0	0
Ditch	Lineville Road	Lineville Road	22	5	32	28	8	6	361	6
Agricultural	Little Suamico	Allen Road Trib.	9	7	24	7	11	0	13	0
		HWY S. Trib.	13	1	33	6	10	0	93	0
Agricultural	Pensaukee	North Branch	0	11	25	15	25	7	541	8
		Wood Road Trib.	10	10	24	23	7	26	91	30
		Spring Creek	9	7	16	25	8	5	232	5
Agricultural	Suamico	South Branch	10	6	28	9	11	0	10	0
		Haller Creek	9	10	38	13	9	0	10	0
–	Kayes Cr.	Lower Kayes Cr.	–	10	–	25	–	–	–	–
–	Heins Cr.	Lower Heins Cr.	–	4	–	–	–	–	–	–
–	Sheboygan R.	Lower Sheboygan	–	9	–	–	–	–	–	–
–	Green Bay	Lower Green Bay	14	–	–	–	–	–	–	–

sites offered suitable flooded riparian habitats or wetlands, and fishery managers had observed breeding in all six basins during previous years. Qualitative adult surveys (30 minute visual searches) began shortly after tributaries were ice-free in March, and ended with the onset of YOY emigration in May.

For YOY production surveys and known-origin otolith collections, we used box traps adapted from Wisconsin Department of Natural Resources YOY monitoring protocols (Paoli, 2012). We deployed YOY box traps just above confluence points downstream of known spawning grounds in each of the ten focal sub-basins. At each site, multiple traps were positioned side-by-side across the entire stream channel (<2 m total width) to capture drifting YOY moving downstream; there is no chance that they could have moved upstream after hatching. Instead, these relatively immobile fish are necessarily moving downstream from their birth site. Box traps were deployed shortly after adults emigrated from breeding grounds, and were checked every two days until no YOY were collected for at least seven consecutive days (or streams dried). This monitoring enabled us to compare the relative timing and productivity of recruitment among sub-basins. While we aspired to collect all YOY produced in a given site we cannot be certain that all YOY were caught. Therefore, this effort represents a quantitative metric of YOY production; not an absolute census. Failure to capture YOY at a site below observed spawning grounds was interpreted as recruitment failure.

To assess the natal homing tendencies of northern pike, we compared the chemistry of the otolith core (the primordia and earliest growth) of adults to YOY sampled from the same sub-basin. Otoliths were collected from emigrating YOY caught in box traps in each sub-basin and year (when sufficient YOY production occurred). After observing spawning behavior at each sub-basin, we collected nine to twenty emigrating adults with fyke nets placed immediately downstream of observed spawning sites. A few additional large adults were donated by anglers (minimum total length of 61 cm). We collected only post-spawn adults; a fish was considered to have spawned if we observed sparring scars on males and if females were partially or fully spent. To place otolith chemistry within our study area into a broader context, we also sampled spawning adult pike from three tributaries outside the study area (5 to 300 km of shoreline distance) as well as offshore in Green Bay before the spawning season began (unknown spawning areas; Table 1).

Otolith preparation and data analyses

Sagittal otoliths were removed using Teflon-coated tweezers and triple-rinsed with ultra-pure water prior to and after sectioning and polishing. Whole adult otoliths were mounted in Buehler's EpoxiCure® epoxy, sectioned along the transverse axis through the origin, adhered to petrographic slides with Crystal Bond® glue, and polished with increasingly fine aluminum oxide powder until the core and each annulus was clearly visible. For YOY otolith samples, an entire otolith was affixed to a petrographic slide using Crystal Bond® and polished until the primordium (component of the otolith that contains any possible maternal input from yolk sac, and therefore is not likely representative of the environmental chemistry) and daily rings were readily visible.

Otoliths were analyzed by laser ablation (Cetac LSX213) inductively coupled plasma mass spectrometry (Perkin Elmer ELAN DRCII) at the GeoMed Analytical Laboratory at the University of Massachusetts in Boston. To characterize natal chemistry of adults, otoliths were sampled with a 150 μm spot size centered on the core (300 pulses at pulse rate of 20 Hz, 100% laser energy). YOY otoliths were ablated using a diametrical transect line (edge-primordium-edge) at a scan rate of 5 μm/s (pulse rate of 20 Hz, 100% laser energy). Mass spectrometer data were integrated approximately every 1 s. Two calcium carbonate standards (USGS MACS-1 and MACS-3) were analyzed every six samples for calibration and drift correction. Each sample was background-corrected for the argon carrier gas measured before ablation. Calcium (^{46}Ca) was

used as an internal standard to control for signal variation (ESM Table S2). To test for maternal influences on otolith chemistry, we compared results from laser transects of YOY otoliths from the edge to just outside the primordia (but excluding the primordia itself) versus similar transects that also included the primordia using multivariate analysis of variance (MANOVA). Additionally, we compared the area of YOY primordia to the area of 150 μm spot used to quantify adult natal core chemistry by measuring the primordium area of YOY using a compound microscope (10×) and imaging software (Nikon's NIS-Elements D). Finally, we compared the overall size of YOY otoliths to that of adult core samples (150 μm diameter).

Eight elements were analyzed, and concentrations were calculated for adult cores and YOY transects using AMS software (Mutchler et al., 2008). Elemental concentrations were expressed as a ratio against Ca. Only five elements (Mg, Ba, Mn, Sr, Zn) were deemed informative for statistical analysis based on concentrations well above background levels and palindromic consistency on both sides of the primordium for YOY. As an added precaution, each YOY was represented as the average of 15 s of laser ablation starting just outside the primordium, thereby avoiding any potential maternal effects at the primordium (Brophy et al., 2004; Chittaro et al., 2006) or variation in the duration of the signal measured from YOY of different ages. Before statistical analysis, we excluded outliers from the dataset by eliminating YOY or adult pike that were >3 SD from their site mean for any element. This criterion resulted in discarding 6.25% of YOY (13 of 208) and 3.8% of adult samples (9 of 233) (Table 1). In order to estimate the age of each YOY, we read daily growth rings within the otolith using a standard compound microscope.

Spatial interpretation of otolith chemistry

Our otolith sampling was designed to test the spatial scale at which chemical differences among breeding areas can be differentiated reliably. Using YOY of known origin, we tested the temporal stability of otolith chemistry at three hierarchical spatial scales (sub-basin, basin, and tributary class) across sampling years using a nested MANOVA. To assess elemental differences within and among basins and tributary classes, we used ANOVA followed by Tukey's HSD pairwise comparisons. Principal component analysis (PCA) of YOY chemistry was used to visualize spatial patterns at each spatial scale. We conducted quadratic discriminant function analyses (QDFA) to evaluate the consistency of differences in chemistry among our three spatial scales. These statistical differences among known-origin YOY provide the foundation for inferring the birthplace of adults from their otolith chemistry.

Homing tendencies were evaluated by comparing the tributary class where an adult was captured to the tributary class where QDFA assignment indicated it was born. We used the discriminant function from QDFA of known-origin YOY otolith chemistry to assign the otolith core chemistry of adults to putative natal habitats. Assignments were at the scale of tributary classes, which were the most informative spatial scale of variation in YOY otolith chemistry. To avoid forcing assignments when adult data were a poor fit to all tributary classes, we considered adults to be unassigned if the posterior probability of classification was <65%.

To place the chemical differences among our focal basins into a regional context, we compared core chemistry of adults from tributaries within versus outside our focal area. ANOVA and Tukey HSD pairwise comparisons were used to determine which elements best discriminated among sites at these larger spatial scales.

Muscle isotope and age comparisons among adults

We surveyed age distributions and muscle stable isotope ratios of adults captured after breeding to test for differences among focal basins that might suggest distinct subpopulations within the study area. To compare age distributions among tributaries, we estimated the birth-

year for each adult pike sampled for otolith chemistry. Independent age estimates from each polished otolith were made by two experienced readers. Discrepancies were rare, and those otoliths were re-read together by both readers to reach consensus.

To test for differences in habitat use outside of the breeding season, we analyzed stable isotopes of C and N from white muscle of adults from each focal basin (n = 5 per basin). The muscle was excised just below the dorsal fin, oven-dried (60 °C for 48 h), ground to a fine powder, sub-sampled (1.3 mg), and analyzed at the Cornell Stable Isotope Laboratory. Results were expressed using the standard $\delta^{15}N$ and $\delta^{13}C$ notation in units of ‰ (Fry, 2007). We used ANCOVA to test for differences between basins while accounting for fish length as a covariate that could reflect size-specific diet patterns. All statistical analyses were conducted using R 2.15.1 (R Core Team, 2012).

Results

Spatial distributions of adult breeders and YOY

Field surveys revealed extensive variation among sub-basins in both adult spawning activity and larval production. While Pensaukee River, Lineville Road Ditch, and Brown Road Ditch received roughly comparable levels of adult spawning activity in both years, far fewer adults were observed in 2012 within Suamico, Little Suamico, and Duck Creek basins compared to 2011 (61% reduction, Table 1). In 2012, Green Bay experienced low winter precipitation and an early spring thaw following unseasonably warm temperatures, bringing tributary discharge down to base flow seven weeks earlier than in 2011 (ESM Fig. S1). Low water levels at the peak of spawning migrations and lack of spring precipitation made many sub-basins wholly or partially inaccessible to adults in 2012. Thus, most spawning activity and YOY production occurred in middle to lower reaches of each basin with the exceptions of the Pensaukee and Suamico Rivers. Moreover, spawning in 2012 often occurred in channels with less aquatic vegetation than the flooded riparian zones that were preferred in 2011, and we observed desiccation of eggs and YOY more often in 2012 than 2011. In total, our network of larval traps captured 24 times more YOY reaching Green Bay in 2011 than in 2012 (Table 1). These emigrating YOY varied from 10 to 103 days old and from 12 to 119 mm total length.

The Pensaukee River was the only basin to produce YOY recruits in all studied sub-basins in both years; all other basins experienced recruitment failures in at least one sub-basin during one or both years. Brown and Lineville Road Ditches were notable for attracting adult breeders, providing spawning habitat, and enabling YOY to grow well in nursery areas in 2012, yet yielding few recruits to Green Bay. Most YOY born in ditches in 2012 became desiccated as water levels receded rapidly during May, leaving culverts dry and isolating wetlands from the ditch channel. In contrast, consistent precipitation in 2011 allowed YOY from all tributaries to move downstream throughout the spring. Overall, YOY trapping in both years indicated that natural rivers draining agricultural areas were more likely to produce recruits that reach Green Bay than the urbanized river or man-made ditches.

Chemical differences among natal areas

MANOVA analyses of known-origin YOY otoliths revealed no consistent sub-basin or basin elemental signatures and only weak QDFA predictive power (14–45% reclassification success). Thus, we could not test the natal homing tendencies of adult northern pike at a finer scale than tributary classes. Among tributary classes, which reflect broad differences in surficial geology and land uses, agricultural, ditch, and urban classes exhibited moderate to high differentiation in YOY otolith chemistry; QDFA reclassification success was 86.5, 73.0, 60.0%, respectively. Of the 10 YOY born in urban Duck Creek, three were misclassified to agricultural rivers and one to ditches, while 27% of the 66 YOY sampled from ditch habitats were misclassified (17 to agricultural rivers, one to

urban). Agricultural rivers showed the lowest misclassification rate (13.5% of 119 YOY), and YOY were misassigned primarily to ditches (n = 13) rather than urban streams (n = 3). Though imperfect, chemical differentiation between these three tributary classes (MANOVA, $F_{2,189}$ = 11.021, p < 0.001) and temporal stability within tributary classes (MANOVA, year × class interaction: $F_{2,189}$ = 1.60, p = 0.104) provide a reasonable basis for assessing spatial and temporal variations in adult origins and testing whether adults are homing to the same class of tributary in which they were born.

All five of the trace elements profiled in YOY otoliths were informative with respect to tributary classes. Relatively high magnesium (Mg) concentrations were found in YOY captured in the urbanized Duck Creek compared to agricultural and ditch basins (ANOVA, $F_{2,192}$ = 8.86, p < 0.001). Barium (Ba) showed the strongest differences between the agricultural rivers (low Ba) and ditch (high Ba) tributary classes (ANOVA, $F_{2,192}$ = 34.74, p < 0.001, Fig. 2). Strontium (Sr) also discriminated agricultural (higher Sr) from ditch and urban catchments (lower Sr; ANOVA, $F_{2,192}$ = 7.72, p < 0.001). Manganese (Mn) was informative for distinguishing between all three tributary classes; high Mn concentrations are more indicative of agricultural basins, low concentrations more representative of ditch basins, and the urban basin had intermediate concentrations (ANOVA, $F_{2,192}$ = 15.13, p < 0.001). Zinc (Zn) differentiated between urban (higher Zn) and ditch (lower Zn) basins (ANOVA, $F_{2,192}$ = 3.92, p = 0.021).

Natal origins and homing of adults

We found no significant differences in Mg, Ba, Zn, Sr, and Mn concentrations in YOY otolith material accreted during larval growth when we excluded or included the primordium (MANOVA $F_{1,5}$ = 0.89, p = 0.49, n = 30). The area of the YOY primordia relative to the laser-ablated 150 μm adult core spot area ranged from 0.6% to 4.6% with a mean of 1.64%. Thus, there was no evidence of strong maternal signatures in pike otoliths that would complicate comparison of the core of adult otoliths (including the primordium) against the post-primordium portion of YOY otoliths in order to assess the natal chemical environment of adults. However, the radius of YOY otoliths averaged 40% of the radius of the adult core spot samples (range 7–92%, n = 180), indicating that the chemistry of adult cores could include some lake influence in addition to material accreted prior to leaving the natal stream.

Of the 185 adult pike whose otolith cores were analyzed, 36% were assigned to agricultural rivers, 33% to ditch habitats, and 31% could not be assigned to a natal tributary class with >65% confidence based on known-origin YOY chemistry. No adults were inferred to have been born in urbanized Duck Creek (Fig. 3). These tributary class assignments were based on multi-element comparisons, but it was particularly notable that no adult otolith cores had Mg concentrations comparable to YOY from Duck Creek (Fig. 2). Of all assignable adults, 57% were spawning in different tributary classes than their inferred natal origin (53% of males; 61% of females). Among fish originating in agricultural rivers, males and females showed similar patterns of tributary class infidelity (45% and 46%, respectively), but those assigned to ditches showed greater gender differences in infidelity (71% of females and 20% of males). Because tributary classes were the only spatial scale at which robust statistical differences were observed in YOY microchemistry, we could not identify the specific river from which the adults originated.

Overlaying ages of adults upon tributary class assignments, there were no clear differences in year class strength between ditch and agricultural tributaries. Since no adults were inferred to originate in the urban river in either year, recruitment patterns there could not be assessed. The occurrence of unassigned individuals was in similar proportions to agricultural- and ditch-origin adults during most years, with the exception of 2003, 2004, and 2005 when unassignable adults were disproportionately common (ESM Fig. S2).
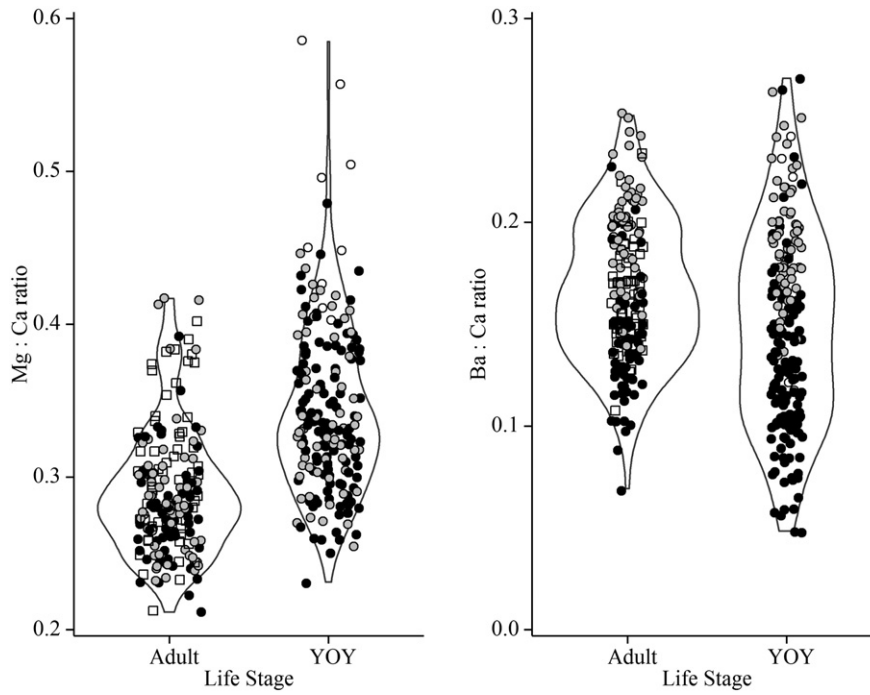
Fig. 2. Patterns of $\log_{10}$ magnesium and $\log_{10}$ barium mass concentrations expressed as a ratio to calcium in pike otoliths sampled from six focal basins. Markers indicate individual young-of-year and adults; polygons represent frequency distributions across all individuals of the same life stage. Marker shading indicates the tributary class where a fish was known (young-of-year) or inferred (adult) to be born: agricultural (black), ditch (gray), urban (open), or unassignable (squares, for adults only). Note that the left panel indicates that all YOY born in the urban tributary class are enriched in magnesium and no adult cores contained similar chemistry. The right panel shows consistent patterns of barium concentrations in both adults and YOYs; adults and YOY originating in agricultural tributaries (black markers) are depleted in barium compared to fish originating in ditch systems (gray markers).

Stable isotope analysis of muscle from spawning adults indicated spatial population structure outside the breeding season. There were significant differences in pike δ^{13}C among basins (ANCOVA, $F_{5,23}$ = 3.51, p = 0.025). Only the northernmost (Pensaukee River) and southernmost (Duck Creek) basins showed significant pairwise differences (Tukey's HSD, p = 0.032), but there was a continuous reduction in
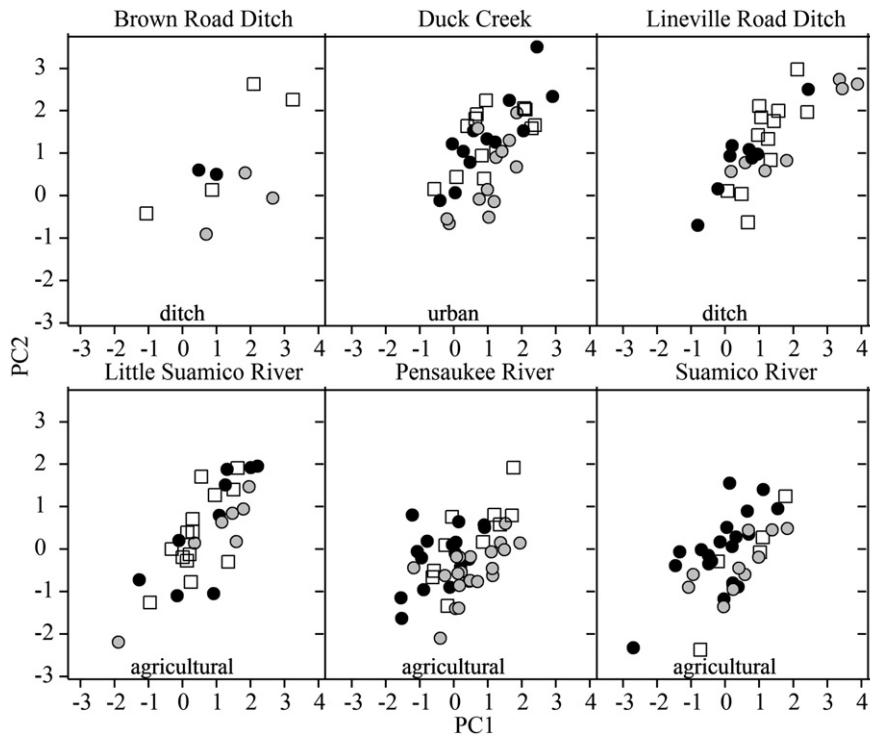
Fig. 3. Principal component analysis of Mg, Ba, Mn, Sr, and Zn within the natal core of adult otoliths in relation to the basin in which spawning occurred, which indicates that pike do not exhibit natal homing in our study area. Markers depict quadratic discriminant function classifications of natal origins as ditches (gray), agricultural rivers (black), or unassignable (open square). Each basin's tributary class is noted at the bottom of each panel. No adults were assigned as originating from within the urban basin (no open markers). PC1 + PC2 explain 59% of variation.

mean δ^{13}C from north to south across all sites (Fig. 4). There were no significant differences among basins in muscle δ^{15}N (ANCOVA, $F_{5,23} = 0.741$, p = 0.600). δ^{15}N increased with fish size across all sites (ANCOVA, $F_{1,23} = 4.73$, p = 0.040), indicating that pike increase in trophic position within the Green Bay food web as they grow. δ^{13}C was comparable among adults assigned to each of the tributary classes (ANOVA, $F_{2,27} = 1.62$, p = 0.216), but there were marginal differences among classes in δ^{15}N (ANOVA, $F_{2,27} = 2.84$, p = 0.076).

Otolith chemistry in the regional context

Comparing otolith core chemistry of adult pike spawning in our six focal basins to that of fish caught in more distant rivers or Green Bay itself indicated that chemical differentiation does not increase predictably with distance. We detected significant overall differentiation between the focal basins and basins that were 5 to 300 km away (MANOVA, $F_{4,228} = 5.74$, p < 0.001). Concentrations of magnesium, manganese, and strontium were informative at these broader spatial scales (ANOVA, $F_{4,228} = 5.37$, p < 0.001, $F_{4,228} = 3.97$, p < 0.05, $F_{4,228} = 10.17$, p < 0.001, respectively), whereas zinc and barium were statistically similar. Interestingly, pairwise comparisons showed clear differences between the focal basins and the rivers that we sampled 5–150 km away (Tukey's HSD, p < 0.05 for Mg, Mn, and Sr), but the most distant basin (Sheboygan River, 300 km away) could not be distinguished from our focal basins using any single element (Tukey HSD, all p > 0.05).

Discussion

Through a combination of detailed field monitoring and environmental chemistry analyses, we have documented enormous spatial and temporal variations in recruitment of northern pike from tributaries of southern Green Bay. Adult pike did not show evidence of natal homing, but rather spawned in all possible types of tributaries irrespective of the tributary class in which they were born. However, YOY recruitment varied strongly among tributary classes and years, indicating that reproductive success of pike is affected both by tributary characteristics and climate. These findings suggest that spawning pike are likely to find new or restored breeding habitats readily, and recruitment success will depend primarily on habitat quality and hydrological stability within migration corridors.

The joint interpretation of our field surveys and otolith chemistry indicates highly skewed contributions of different tributary classes to YOY pike recruitment to Green Bay. Importantly, it appears that adult breeding activity is a poor predictor of contribution to the YOY year class. Despite many adults migrating into the urban basin (Duck Creek), neither YOY trapping nor adult otolith chemistry offered any evidence of successful recruitment. In contrast, both adult breeding activity and YOY production were highest in natural rivers draining agricultural landscapes. These tributaries produced a large majority of recruiting YOY, as well as 52% of assignable breeding adults. The Pensaukee River yielded the most adult observations and YOY produced in both 2011 and 2012. This watershed was the largest in our study in terms of drainage area, and contains the most wetland habitat. The other agricultural basins (Suamico and Little Suamico Rivers) along with the urban basin (Duck Creek) had markedly fewer adult observations, and YOY production decreased in a drought year (2012) compared to a high-flow year (2011).

The role of ditch habitats in supporting pike populations was more enigmatic. We observed substantial adult breeding activity in both ditches during both years, yet these habitats yielded negligible YOY emigration to Green Bay. Nonetheless, otolith chemistry suggested that adult pike were almost as likely to have been spawned in a ditch habitat as a natural river in an agricultural watershed. These conflicting results could imply sporadic recruitment success from ditches, though we found little variation among pike year classes in the frequency of adults inferred to have been born in ditches. Thus, further field observations and otolith chemistry analyses will be required to fully understand pike recruitment from ditches.

Prospects for breeding habitat restoration appear promising for northern pike based on the lack of natal homing even at the tributary class level. Even when urbanized Duck Creek failed to produce recruits, we found that it still receives breeding adults originating from the other two classes of nearby tributaries. Moreover, the combination of a substantial proportion of unassignable adults spawning in our focal basins and distinctive otolith core chemistry of adults sampled from sites outside our study area suggests that spawners at any one site may include fish that were
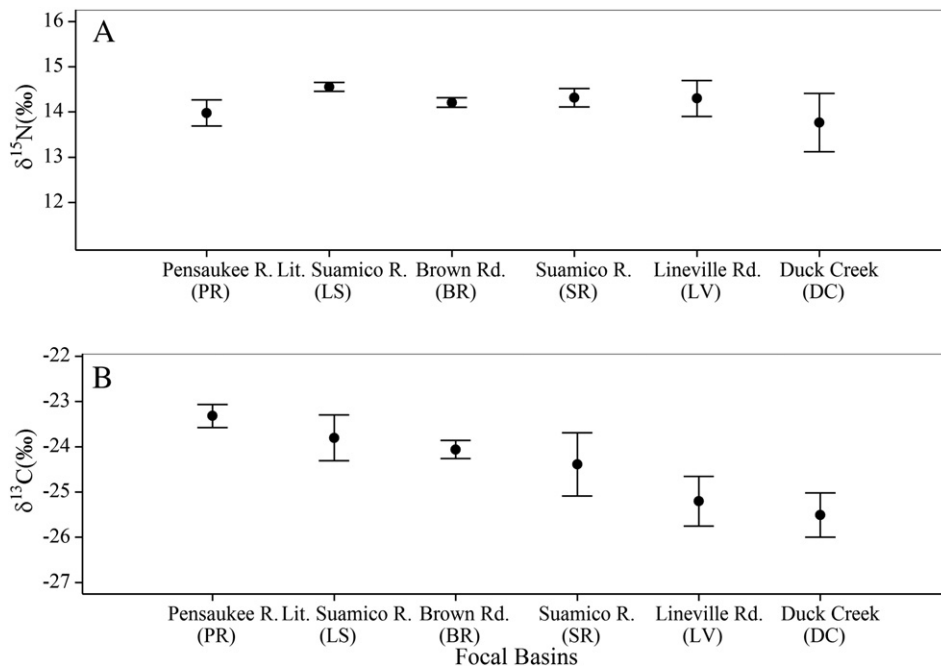

Fig. 4. Stable isotope ratios of muscle tissue from adult northern pike from six focal basins demonstrating (A) no significant differences in δ^{15}N and (B) significant differences in δ^{13}C between the northernmost (PR) and southernmost (DC) basins along a gradient from north (left) to south (right). Dark markers and error bars indicate mean and one S.E. (n = 5 per basin).

born far away. In any case, the fact that adult pike continue to spawn in urbanized Duck Creek despite no evidence of recruitment from that basin strongly suggests that pike are capable of finding and using new spawning areas following habitat restoration or creation efforts, and that seeding of larvae to imprint on those habitats is probably unnecessary.

Our multi-scale analyses, like those of Brazner et al. (2004a,b) and Pangle et al. (2010), provide insight into the spatial scale at which robust inferences from otolith chemistry are possible. Few previous studies have compared otolith chemistry patterns at sub-basin scales, and we observed variability in YOY otolith chemistry in both time (between years) and space within basins. Thus, it would be unwise to try to infer the sub-basin in which breeding pike had been born, even though individual sub-basins were often readily differentiable within a year. In contrast, differences in otolith chemistry at the basin scale were relatively stable between years, but the degree of trace element differentiation was insufficient to reconstruct robust predictions of natal origins among our six focal basins. Despite similar geochemistry among basins in this postglacial landscape, significant differences emerged when basins were grouped into classes based on land use (agricultural vs. urbanized) and stream type (man-made ditch vs. natural river). The influence of urban land use on water chemistry is well known for some metals (Mikkelsen et al., 1997; Paul and Meyer, 2001), and can be reflected in otolith chemistry (Friedrich and Halden, 2010). Most of the elements that we used had already proven informative in previous studies of otolith chemistry in the Great Lakes, albeit at larger spatial scales (Hand et al., 2008; Ludsin et al., 2006; Pangle et al., 2010). Interestingly, our most distant sampling site (Sheboygan River, 300 km away) could not be distinguished from our focal basins, suggesting that convergent multi-element patterns may be inevitable in post-glacial landscapes. Overall, otolith chemistry could not discern between sub-basins, obstructing our ability to track natal origins or population structure among sub-basins or nearby watersheds, but otoliths did offer unique insights at scales of tens to hundreds of km or when human activities altered water chemistry.

Our inferences regarding adult origins depend on the temporal stability of chemical differences among basins. Despite the hydrological differences between 2011 (unusually wet) and 2012 (unusually dry), we found relative temporal stability of YOY otolith chemistry at the scale of basins and tributary classes. Differences were significant despite substantial variability within each annual cohort of YOY collected from a site. Few previous studies have tested temporal variation across sites, but our multi-year study and that of Engstedt et al. (2014) indicate that spatial patterns can exceed interannual differences, allowing statistical inference of natal origin of adults based on matching adult core signatures to maps of variation in YOY otolith chemistry. Future studies should continue to evaluate the temporal stability of these chemical 'fingerprints', particularly across land use gradients that augment natural chemical variation (e.g., high Mg and Zn in urbanized Duck Creek).

We also confirmed that maternal effects in the primordia had minimal effects on overall otolith core chemistry in YOY or adults, validating our comparisons. The otolith primordium has been reported to be enriched in Mg or other elements, reflecting a signature arising from maternal provisioning (Brophy et al., 2004). In pike, we found that the maternally-influenced primordia represents a tiny fraction (<4.6%) of the otolith material ablated from the core of adult otoliths, and including primordia material had no significant effects on any element. We infer that the remainder of our 150 μm adult core spot primarily reflects material accrued by YOY in their natal stream prior to emigrating to Green Bay; our YOY otoliths were substantially smaller on average than the adult core spot, but we sampled these young fish far above the stream outlet so they would continue to grow in the lower reaches of the natal stream prior to reaching the lake (Oele, unpublished data). Thus, the chemistry of post-primordia transects in YOY should be comparable to that of the entire core of adult otoliths if both fish were born in the same location.

Stable isotope ratios of adult muscle tissue revealed that pike do not mix freely in southern Green Bay outside of the breeding season (Fig. 4).

Muscle isotope signatures integrate spatial and dietary variations through time, typically reflecting months of foraging in large fish (Heady and Moore, 2013; McIntyre and Flecker, 2006). This approach has proven useful for elucidating fish habitat use along gradients of nutrient loading, land use, and other factors (e.g., Hoffman et al., 2012; Sepulveda et al., 2009; Thorrold et al., 1998). Statistically significant differences in $\delta^{13}C$ of adult pike breeding in the northernmost versus southernmost basins, along with the clinal gradient between these two endpoints, suggest that most adults are relatively sedentary. The observed patterns of C isotope differences could arise from local differences in the isotope ratios of basal resources underlying lake food webs along the length of Green Bay, or systematic spatial differences in the identity of prey eaten by adult pike (France, 1995; Vander Zanden et al., 2011). Regardless of the mechanism, the non-random pattern of $\delta^{13}C$ suggests that populations of adult pike are spatially segregated within Green Bay. The uniformity in $\delta^{15}N$ among tributaries suggests that trophic position of spawning adults is similar across Green Bay and that the $\delta^{15}N$ of basal resources is also similar. Given the lack of evidence for natal homing, we speculate that northern pike in Green Bay mix freely when young but become fairly sedentary as adults.

The lack of natal homing despite relatively discrete sub-populations of adults suggests little potential for genetic differentiation within pike in our study region. Some migratory fish populations, famously including Pacific salmon (e.g., Beacham et al., 2014; Sato et al., 2004) but also anadromous northern pike in the Baltic Sea (Engstedt et al., 2014; Laikre et al., 2005), show natal homing tendencies that can be strong enough to engender population genetic structure. Given the contrast between our inferences from otolith chemistry inferences (no natal homing) and those from pike in the Baltic Sea (strong natal homing; Engstedt et al., 2014), it appears that natal homing is not a fixed trait in northern pike. Homing could be selected for in the Baltic Sea by the strong salinity cline from north to south, whereby southern salinities can exceed the tolerances of young pike (Jacobsen et al., 2007). Adaptive salinity tolerance could be a powerful selective pressure favoring population differentiation and high-fidelity natal homing. Similarly, local adaptation is widely invoked to explain trans-generational site fidelity in salmonids (Quinn, 2005) and has been implicated as a factor explaining variation in northern pike growth rates across continents (Rypel, 2012). However, it is more difficult to imagine substantial advantages of site fidelity among adjacent tributaries of the North American Great Lakes. Thus, additional assessments of natal homing in other pike populations will be required to identify the selective factors that drive the acquisition or loss of natal homing in northern pike.

Due to the lack of lifelong site fidelity, we infer that any tributary which offers suitable spawning conditions is likely to be colonized by breeding pike. Thus, sites where ecological connectivity or breeding habitats have been restored should not require transfer of young pike in order to imprint, thereby simplifying the requirements for successful restoration. At the same time, our observations of low recruitment of YOY pike from ditch and urban basins suggest that it is essential to ensure that migration corridors allow both adults and YOY to move downstream to reach stable habitats throughout the breeding season. Restoration and management plans which fail to allow fish to return to the lake may cause more harm than good due to both mortality of adults and YOY recruitment failures like those we observed in ditches and urban habitats.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2015.05.003.

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