Management of Biological Invasions (2022) Volume 13, Issue 1: 168–190

Research Article

Mechanism of northern pike invasion in the Columbia River Basin

Kellie J. Carim[1,2,3,*], Lisa A. Eby[3], Loren M. Miller[4], Holly McLellan[5], Virgil Dupuis[6] and Michael K. Schwartz[2]

[1]Aldo Leopold Wilderness Research Institute, U.S. Forest Service, Rocky Mountain Research Station, Missoula, MT 59801 USA
[2]National Genomics Center for Wildlife and Fish Conservation, U.S. Forest Service, Rocky Mountain Research Station, Missoula, MT 59801, USA
[3]Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA
[4]Minnesota Department of Natural Resources, St. Paul, MT 55155, USA
[5]Colville Confederated Tribes, Fish and Wildlife Department, Spokane, WA, USA
[6]Salish Kootenai College, Pablo, MT 59855, USA

*Corresponding author
Author e-mails: kellie.carim@usda.gov

Citation: Carim KJ, Eby LA, Miller LM, McLellan H, Dupuis V, Schwartz MK (2022) Mechanism of northern pike invasion in the Columbia River Basin. *Management of Biological Invasions* 13(1): 168–190, https://doi.org/10.3391/mbi.2022.13.1.10

Received: 24 May 2021
Accepted: 25 August 2021
Published: 29 November 2021

Thematic editor: Matthew Barnes

Abstract

The spread of aquatic invasive species typically occurs through a combination of natural and human mediated dispersal. For many aquatic invasive species, natural dispersal is limited to aquatic corridors connecting habitat. In contrast, human transport may facilitate more distant dispersal and transport among disconnected waterbodies. Genetic information can serve as a powerful tool to track invasion histories and identify both the sources and mechanisms of invasive species dispersal. We used genetic information to understand invasion history and dynamics of expanding northern pike invasion in the Columbia River basin. Results indicate that the initial introduction of northern pike into the Pend Oreille River (in eastern Washington State) resulted from human transport of fish, not dispersal from established populations upstream. Subsequent reproduction and natural dispersal from the Pend Oreille River resulted in downstream expansion of northern pike into Lake Roosevelt, a reservoir within the mainstem Columbia River. These results highlight the need for a holistic approach to suppression of invasive species. Immediate efforts must address the biological mechanisms of natural dispersal. Sustained suppression and eradication must take a broad approach that includes coordination between management agencies, as well as policy and public outreach aimed at prevention of repeated human transport events. The genetic database created from this study has already been used to eliminate potential source populations for new northern pike invasions in Washington State outside the Columbia River basin. This highlights the utility of genetic monitoring for both immediate and long-term applications to managing aquatic species invasions.

Key words: *Esox lucius*, genetic assignment, human transport, isolation by distance

Introduction

Dispersal of invasive fish can be broadly categorized as either natural or human mediated. Natural dispersal of invasive fish is typically restricted to aquatic corridors connecting habitat patches, and the resulting new invasions tend to be near the source population (Havel et al. 2015). In contrast, human transport can facilitate introductions that are more distant and/or disconnected from the source population, resulting in more rapid spread relative to natural dispersal (e.g., Jackson and Grey 2013; Ricciardi 2006). For most aquatic invasive species, invasion histories include a combination of both dispersal mechanisms (Blackburn et al. 2011). Efforts to control an invasive fish population will be most successful if they are tailored to the unique combinations of dispersal mechanisms driving the invasion (Epanchin-Niell and Hastings 2010). For example, mitigating natural dispersal may require suppression of source populations to prevent repeated invasions (Britton et al. 2011; Epanchin-Niell and Hastings 2010). Human mediated dispersal of fish is often intentional (Strayer and Dudgeon 2010) and mitigating this mechanism requires tactics beyond biological control, such as public education, policy, interagency collaboration, and other human dimension related actions aimed at prevention (Ricciardi et al. 2017). Information that describes the invasion history and dispersal mechanisms promoting expansion is therefore critical for effectively controlling an invasion (Epanchin-Niell and Hastings 2010).

Genetic information has frequently been used to describe dispersal mechanisms and reconstruct invasion history of nonnative species (Cristescu 2015). This is possible because dispersal mechanisms are reflected in patterns of genetic diversity, population structure, and relatedness across the landscape. For example, natural dispersal of invasive fish in streams and river may follow a “stepping-stone” pattern of dispersal where populations expand downstream through connected river corridors. Under a stepping-stone model, relatedness between populations typically declines with geographic distance (Allendorf et al. 2012; Kimura and Weiss 1964; Slatkin and Maddison 1990). In contrast, human transport of invasive species may result in populations whose genetic relatedness is not correlated with proximity or habitat connectivity. Frequency of dispersal and connectedness of populations may also be reflected in genetic patterns. Lower genetic diversity is common in new populations where a small number of founders from one or a very limited number of sources are responsible for the gene pool (Allendorf et al. 2012; Roman and Darling 2007; Slatkin and Excoffier 2012). If dispersal from source populations occurs frequently, these “founder effects” will degrade as new migrants boost genetic diversity (Roman and Darling 2007). If dispersal from source populations occurs infrequently, the new population will undergo genetic drift, maintaining lower levels of diversity and further diverging from source populations over time (Allendorf et al. 2012; Roman and Darling 2007). In addition to tracking invasion histories, genetic information can be compiled into a database and used to assess the routes of novel introductions. For example, Signorile et al. (2016) compared genotypes of individuals in newly detected populations of invasive American Eastern grey squirrel (*Sciurus carolinensis*) in Europe to a genetic database of over 1400 individuals from 59 locations across Europe and North America. These comparisons identified several instances of illegal human transport of this species, including the routes of illegal trade pet trade in Italy. By combining genetic information with data on habitat connectivity and historical observations, biologists can more accurately infer invasion routes and dispersal mechanisms (Handley et al. 2011), which in turn can guide efforts to control invasive species. The upper Columbia River of western North America is one area where managers are actively working to mitigate current and new invasions of numerous nonnative species (Rahel 2000; Sanderson et al. 2009; Sol et al. 2021).

Northern pike, *Esox lucius* (Linneaus, 1758), is a nonnative species of the upper Columbia River that has been raising management concern in recent years. The native range of northern pike is Holarctic and includes portions of Canada and the United States (Page and Burr 2011). As a popular sport fish, they have been introduced outside their native range, including areas of southeastern Alaska, southwestern Canada, and the western contiguous United States (Dunker et al. 2018). Northern pike are highly piscivorous (Craig 2008), and introductions of this species have been linked to declines in native fish populations, including populations of sensitive species in the Columbia River basin (He and Kitchell 1990; Muhfled et al. 2008; Ostovar 2012; Sepulveda et al. 2013, 2015). Nonnative northern pike have been present in the headwaters of Columbia River for over 65 years (McMahon and Bennett 1996), but a sudden, rapid expansion of invasive northern pike into the mainstem Columbia River over the last decade has raised concern.

The early invasion history of the northern pike in the Columbia River basin is poorly understood. Fisheries managers believe northern pike were introduced to western Montana in the mid-1900's through a combination of human transport (including legal stocking and illegal introductions) and subsequent dispersal (McMahon and Bennett 1996; Great Falls Tribune 1986). By the 1970's established populations of northern pike were present in the Clark Fork River basin (Montana) and Coeur d'Alene River basin (Idaho; Figure 1a). Throughout these basins, hydroelectric dams block upstream passage of fish, but there are no barriers to downstream movement (Figure 1b). Through the 1990's, managers observed little to no change in the distribution of northern pike in these drainages. In 2004, managers captured the first northern pike in the Pend Oreille River of eastern Washington during standardized fish surveys (Bean at al. 2011). Lake Pend Oreille (Idaho) is the nearest waterbody upstream of the Pend Oreille River. Anecdotal observations of northern pike in the lower Clark Fork River (below Cabinet Gorge Dam; Figure 1b) and Lake Pend Oreille date back to the 1970's, however the first sighting in Lake Pend Oreille documented by fisheries managers did not occur until 2009 and remained at low densities through the 2010's (Watkins et al. 2019; M. Corsi *personal communication*). The simplest explanation for expansion of northern pike into eastern Washington is that fish dispersed from the nearest upstream sources. However, the rare occurrence of northern pike in the lower Clark Fork River and Lake Pend Oreille through the early 2000's casts doubt on the likelihood that this population is the source of the recently invaded areas downstream.

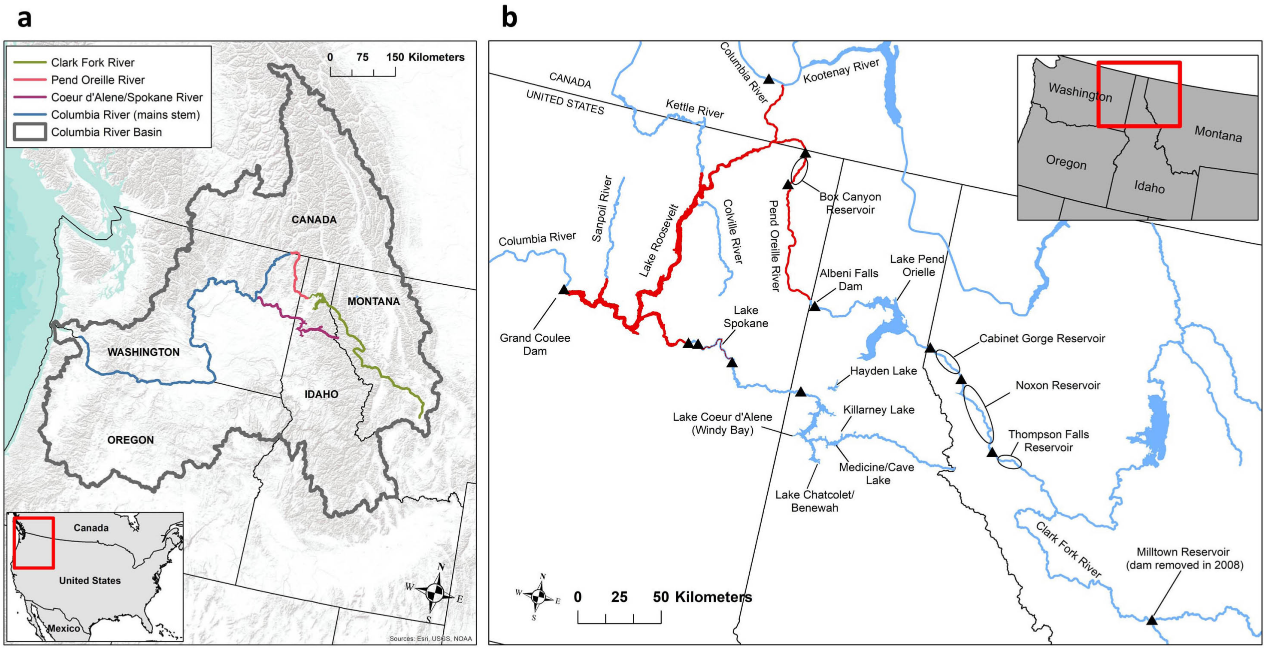

Figure 1. Study area map showing (a) the Columbia River basin and major rivers drainages in this study and (b) waterbodies with populations of northern pike sampled in this study. In (b), black triangles represent hydroelectric dams that prevent upstream movement of fish. Waterbodies in red are primarily located in eastern Washington, USA, and represent the most recently invaded areas.

Expansion of northern pike into downstream waterbodies occurred rapidly following the observation in the Pend Oreille River of Washington. By 2010, northern pike had become established in the main stem of the Columbia River in Canada and the United States (Lee et al. 2010). Currently, the leading edge of the northern pike invasion in the region sits at the lower end of Lake Roosevelt, a reservoir created by Grand Coulee Dam in the upper Columbia River of eastern Washington (Carim et al. 2019; McLellan et al. 2019; Figure 1b). To thwart expansion, state and tribal biologists have been actively suppressing northern pike in eastern Washington, including the Pend Oreille River and Lake Roosevelt (Lee and Parsons 2020; McLellan et al. 2018, 2019). Intensive gill netting efforts have been successful at reducing northern pike abundance in some areas, including the Pend Oreille River (Harvey and Bean 2020). However, occurrence of northern pike near Grand Coulee Dam (the lower end of Lake Roosevelt) has increased over the last several years (McLellan et al. 2018, 2019) and expansion beyond Lake Roosevelt appears imminent. Managers fear that expansion beyond Lake Roosevelt would compromise recovery efforts for over a dozen stocks of Pacific trout and salmon listed as Threatened or Endangered under the Endangered Species Act (National Marine Fisheries Service 2016). Information on the source of northern pike in eastern Washington and mechanisms driving expansion is needed to ensure that management efforts are effective at containing the current population of northern pike in Lake Roosevelt and preventing repeated or novel introductions from established populations in the region.

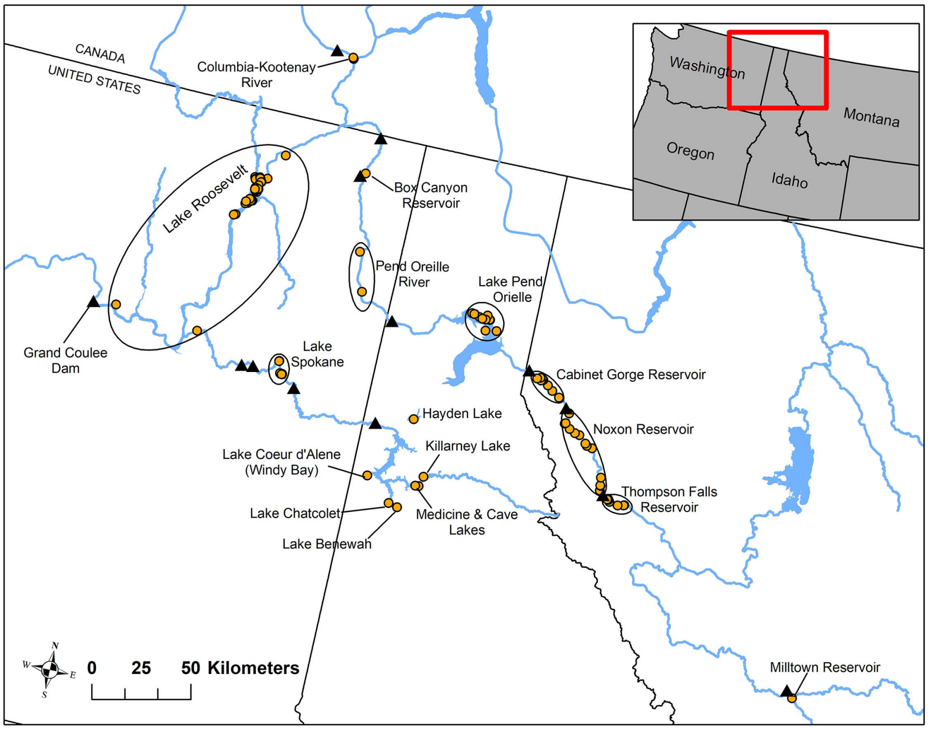

Figure 2. Sampling locations for northern pike in this study. Grey triangles represent hydroelectric dams that prevent upstream movement of fish. Yellow dots represent northern pike sampling locations.

In this study, we aimed to address this knowledge gap through three research objectives. First, we used genetic assignment to identify original source population(s) and dispersal mechanisms (natural dispersal vs human transport) responsible for the invasion into eastern Washington. Second, we assessed population structure and used genetic assignment to understand the mechanisms of expansion locally at the leading edge of the invasion in Lake Roosevelt. Finally, we combined information from the first two objectives to reconstruct the invasion history (i.e., the pattern of expansion) from the source population through all waterbodies in eastern Washington. In the process of addressing these objectives, we assembled a genetic database that captures the genetic diversity and structure of northern pike populations in the Columbia River basin. This database can be used to identify or exclude sources and routes of novel invasions in the region, allowing managers to mount a more targeted response.

Materials and methods

Study area

To understand the relatedness of northern pike populations across the upper Columbia River basin, we worked with local fisheries managers to obtain tissues of northern pike from 17 waterbodies in three major river drainages in the upper Columbia River basin (Figure 2, Table 1) These drainages included two river basins with potential source populations, and a third representing recently invaded waterbodies in eastern Washington

Table 1. Waterbodies sampled for northern pike in this study. For each drainage, waterbodies are listed from upstream to downstream order. Note that individuals from Medicine and Cave Lakes, as well as Lake Benewah and Lake Chatcolet are grouped for genetic analysis.

River Basin	Waterbody	Sample Size	Year Collected	Allelic Richness
Northern Pike Established				
Clark Fork River	Milltown Reservoir	27	2000, 2003, 2004	2.54
Clark Fork River	Thompson Falls Reservoir	24	2016	3.55
Clark Fork River	Noxon Reservoir	25	2016	3.27
Clark Fork River	Cabinet Gorge Reservoir	24	2016	3.36
Clark Fork River	Lake Pend Oreille	50	2018, 2019	3.09
Coeur d'Alene River	Killarney Lake	8	2019	2.91
Coeur d'Alene River	Medicine Lake	13	2018	3.08
Coeur d'Alene River	Cave Lake	12		
Coeur d'Alene River	Lake Benewah	28	2019	2.86
Coeur d'Alene River	Lake Chatcolet	24		
Coeur d'Alene River	Lake Coeur d’Alene	27	2018	3.04
Coeur d'Alene River	Lake Spokane	27	2018	2.54
Coeur d'Alene River	Hayden Lake	17	2019	2.36
Northern Pike Recently Invaded				
Pend Oreille River	Pend Oreille River	36	2016	2.11
Pend Oreille River	Box Canyon Reservoir	25	2016	2.08
Columbia River	Columbia-Kootenay River confluence	7	2018	1.64
Columbia River	Lake Roosevelt	77	2016, 2017, 2018	1.89

(i.e., those invaded since 2004). The first drainage spans portions of the lower Clark Fork River basin from the confluence of the Blackfoot and Clark Fork rivers in western Montana to Lake Pend Oreille. Waterbodies sampled in the Clark Fork River basin include Milltown Reservoir, Thompson Falls Reservoir, Noxon Reservoir, Cabinet Gorge Reservoir and Lake Pend Oreille. Each reservoir is separated by a dam preventing upstream movement of fish. Note that Milltown Dam, which created Milltown Reservoir at the confluence of the Blackfoot and Clark Fork Rivers, was removed in 2008. The dam removal and subsequent river restoration eliminated the northern pike habitat and the associated population (Hammer and Hughes 2011; Schmetterling et al. 2015). The second drainage area includes the Coeur d’Alene River and Spokane River basins (hereafter, Coeur d’Alene River basin). Waterbodies sampled in this river basin include Killarney Lake, Medicine Lake, Cave Lake, Lake Benewah, Lake Chatcolet, Lake Coeur d’Alene, Lake Spokane (a reservoir within the Spokane River), and Hayden Lake. These waterbodies are physically connected with two exceptions. First, upstream movement of fish from Lake Spokane to Lake Coeur d’Alene is blocked by two dams (Figure 1b). Secondly, Hayden Lake is an isolated lake with no outlet and is located approximately 11 km overland from Lake Coeur d’Alene. The third drainage represents the recently invaded waterbodies, including the Pend Oreille River downstream of Albeni Falls Dam in eastern Washington State, Box Canyon Reservoir (a reservoir within the Pend Oreille River), the mainstem Columbia River, and Lake Roosevelt. Lake Roosevelt is a reservoir within the Columbia River formed by Grand Coulee Dam and contains the leading edge of the northern pike invasion.

Sample collection and processing

Tissues of northern pike from all waterbodies were collected opportunistically between 2000 and 2016 by local tribal or state fisheries managers during gill net surveys and suppression efforts (Figure 2; Table 1). For each sample, a portion of the fin was clipped and preserved on chromatography paper. The date and location of capture, and total length (mm) was recorded for each fish. Tissues were sent to the U.S.D.A. Forest Service Rocky Mountain Research Station's National Genomics Center for Wildlife and Fish Conservation in Missoula, MT, USA, for analysis. All tissues were handled under tissue use protocol TU004-18LEECS-091918 approved by the University of University of Montana Institutional Animal Care and Use Committee. The number of individuals analyzed from each waterbody ranged from 7 to 77. We aimed to analyze a minimum of 25 fish per population, but waterbodies with lower fish densities and capture rates tended to have smaller sample sizes.

DNA was extracted using a Qiagen Blood and Tissue Kit and following manufacturer's protocols. DNA was diluted 1:10 in H_20 and amplified across 11 polymorphic microsatellite loci: EL05, EL15, EL20 (Ouellet-Cauchon et al. 2014), Elu19 (Miller and Kapuscinski 1997), B24, B25, B117, B259, B422, B451, B457 (Aguilar et al. 2005). Details of fluorescent labels, multiplexing, and modifications to primers (e.g., addition of tails) can be found in Tables S1 and S2. Polymerase chain reaction (PCR) amplification occurred in 15 µl reactions consisting of 5 µl DNA template diluted 1:10 inH_2O 0.5 U AmpliTaq Gold, 0.33 µM primer master mix, 0.2 mM dNTPs, 1X buffer, 1.25 mM $MgCl_2$, and 4.95 µl H_2O. PCR cycling conditions began with 15 min at 95 °C, followed by 42 x [30 sec at 95 °C, 90 sec at 50 °C, and 60 sec at 72 °C], 30 min at 60 °C, and then held at 12 °C. PCR products were visualized on an ABI3130xl Genetic Analyzer (Applied Biosystems Inc., Foster City, CA) at the Genetics CORE Facility at the University of Montana, Missoula, USA. Allele sizes were determined using the ABI GS500LIZ ladder, (Applied Biosystems Inc., Foster City, CA). Chromatogram output was viewed and analyzed using Geneious 10.0.9 (https://www.geneious.com).

Statistical analysis

Individuals were initially grouped by waterbody of capture, resulting in a total of 17 groups (Table 1). For each group, we used Genepop on the Web (Raymond and Rousset 1995; Rousset 2008) to test for deviations from Hardy-Weinberg expectation and linkage disequilibrium. We used HPRare (Kalinowski 2005) to estimate allelic richness. The smallest population size in this study was 7 (Columbia-Kootenai River confluence) and only two other populations had sample sizes lower than 24 (Killarney and Hayden Lakes). To avoid scaling to small sample sizes, we estimated allelic richness for all populations (with groupings described below) using rarefaction to scale the sample size to 24 individuals, recognizing that estimates will be biased low for smaller sample sizes.

Given habitat continuity, it appeared ecologically appropriate to group fish from two pairs of connected waterbodies in the Coeur d'Alene River basin into single populations for genetic analyses. Both Medicine and Cave Lakes and Lakes Benewah and Lake Chatcolet are adjacent pairs of waterbodies connected by continuous habitat for northern pike, characterized by shallow water depths and emergent vegetation. Additionally, mark-recapture studies conducted by the Coeur d'Alene Tribe of Indians in Lake Chatcolet and Lake Benewah show regular movement of northern pike throughout these sections (Firehammer and Vitale 2020). To determine if the data supported combining these pairs of samples, as well as spatial genetic structure among northern pike in this system, we estimated pairwise Fst values for all populations in Arlequin (Excoffier and Lischer 2010).

Objective 1: Source of Northern Pike into Eastern Washington Waters

To look for general structure and relatedness of populations in the dataset we performed a principal coordinates analysis in GenAlex (Peakall and Smouse 2006, 2012) using a covariance matrix with standardization. We performed genetic assignment in GeneClass2 (Piry et al. 2004) to determine the probability that each established population in our dataset (n = 11, Table 1) was the source of fish in recently invaded waterbodies of eastern Washington (n = 145, including fish from Pend Oreille River, Box Canyon Reservoir, Kootenai-Columbia confluence, and Lake Roosevelt). Individuals from recently invaded waterbodies were assigned to potential reference (source) populations using the frequency-based computation criterion (Paetkau et al. 1995) and the simulation algorithm developed by Paetkau et al. (2004) with 100,000 iterations. Using these settings, the probability that an individual originated from a reference population is calculated based on the following steps. First, the program draws from a potential source population to simulate multilocus genotypes for a large number of individuals. The likelihoods of these genotypes being encountered in a potential source population is calculated based on the source population's allele frequencies. The assignment probability for an observed individual is calculated as the rank of its corresponding likelihood within the distribution of likelihood values from simulated genotypes (Cornuet et al. 1999; Rannala and Mountain 1997).

Finally, fish in the newly invaded areas should represent a subset of the alleles present in the source population(s). Therefore, we also compared the alleles observed in the newly invaded area with those observed in the Clark Fork and Coeur d'Alene River basins to look for patterns that would suggest the likely source.

Objective 2: Pattern of Expansion at Leading Edge of the Invasion

To examine the pattern of spread at the leading edge of the invasion, we used STRUCTURE (Pritchard et al. 2000) to look for population sub-structuring among individuals captured in recently invaded areas (the Pend Oreille River downstream through Lake Roosevelt). We tested the most likely number of populations from K = 1 to K = 10 with five repetitions for each value of K, and a 100,000 burn in period followed by 500,000 iterations for each run. If K = 1, that would mean all recently invaded waterbodies would represent one single population. If K = 3, then each of the recently invaded waterbodies sampled would represent a distinct population. We tested up to K = 10 to ensure that the true number of populations was included in our analyses. To determine most likely source of individuals in Lake Roosevelt, we performed another genetic assignment in GeneClass2 (Piry et al. 2004). In this analysis, individuals from Lake Roosevelt (n = 77) were assigned to reference populations using the frequency-based computation criterion (Paetkau et al. 1995) with 100,000 iterations as described above. All 15 study populations (n = 11 established and n = 4 recently invaded; Table 1) were included as reference populations. Including Lake Roosevelt as a reference population allowed fish to "assign to self", testing for local reproduction and dispersal as a mechanism of the expansion in this waterbody.

Objective 3: Reconstructing the Invasion History

We used DIYABC v2.1 (Cornuet et al. 2014) to assess invasion scenarios from potential source populations to recently invaded waterbodies. This program infers population history via approximate Bayesian computation. The program uses input information on population and genetic parameters to simulate a larger number of datasets for different user-defined population histories or "scenarios". Simulated datasets are then compared to the true dataset to identify the most likely scenario.

Drawing upon information from the genetic assignment analyses above, we compared four invasion scenarios (Figure 3). To increase confidence in results and decrease computation times (Cabrera and Palsbøll 2017), we used results from Objective 1 to inform development of these four scenarios. Specifically, we grouped fish from Pend Oreille River and Box Canyon Reservoir into one population and modeled these as the source of fish in Lake Roosevelt (see results below). Fish from the Columbia-Kootenay River confluence were not included in this analysis due to the small sample size (n = 7) from this location. The four scenarios tested were:

> **Scenario 1:** Medicine-Cave Lakes share a common ancestor with Lake Pend Oreille and was the source population for fish in the Pend Oreille River-Box Canyon Reservoir. Box Canyon Reservoir was in turn the source of fish in Lake Roosevelt (Figure 3a).

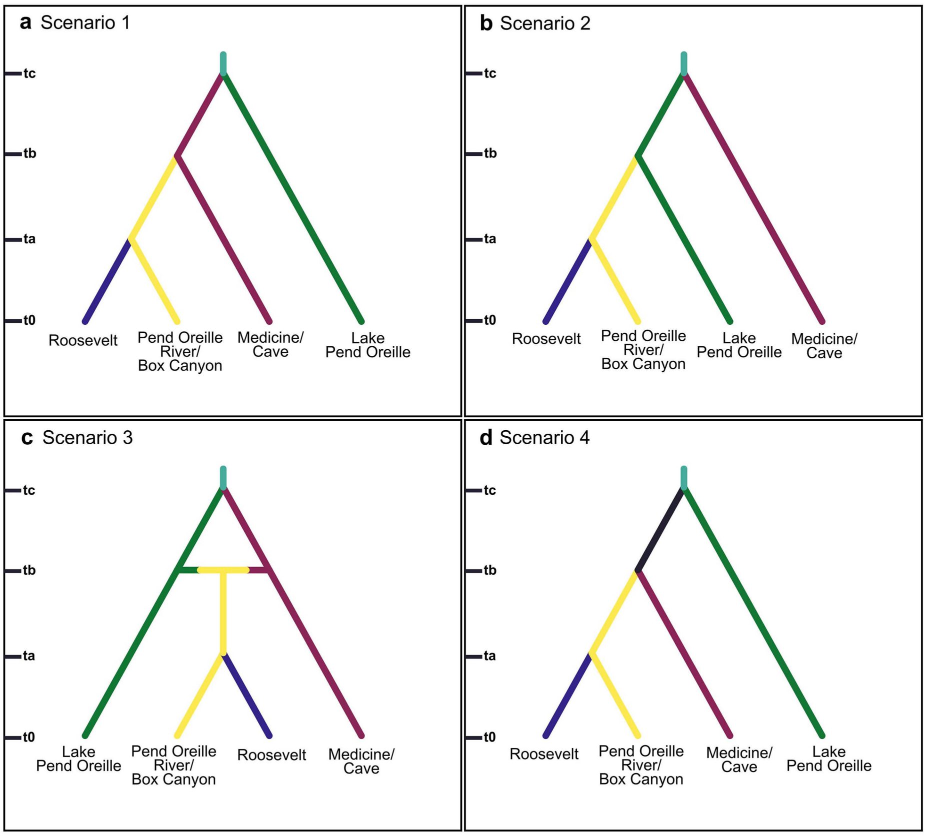

Figure 3. Invasion scenarios of northern pike in the Columbia River basin compared using microsatellite data in DIYABC. In all scenarios, the Pend Oreille River was the source of fish in Lake Roosevelt. In Scenario 1 (a), Medicine-Cave Lakes share a common ancestor with Lake Pend Oreille, and Medicine-Cave Lakes were the source of fish to the Pend Oreille River. In Scenario 2 (b), Medicine-Cave Lakes share a common ancestor with Lake Pend Oreille, but Lake Pend Oreille was the source of fish to the Pend Oreille River. In Scenario 3 (c); Medicine-Cave Lakes share a common ancestor and admixture of the two was the source of fish in the Pend Oreille River. In Scenario 4 (d), Lake Pend Oreille shares a common ancestor with an unsampled population. The unsampled population was the source of fish to both Medicine-Cave and the Pend Oreille River. Timelines on the left side of each scenario mark the point of coalescent events; all samples were collected at t0.

Scenario 2: Similar to Scenario 1, except Lake Pend Oreille served as the source population to fish in the Pend Oreille River-Box Canyon Reservoir (Figure 3b).

Scenario 3: Fish in the Pend Oreille River-Box Canyon Reservoir were the product of admixture between two source populations. Specifically, they were the combined product of a translocation from Medicine-Cave Lakes along with downstream movement of fish from Lake Pend Oreille (Figure 3c).

Scenario 4: Medicine-Cave Lakes were not a direct source of fish to Pend Oreille River-Box Canyon Reservoir, but rather are related to the true source population that was not sampled in this study. Here, an unsampled population shared a common ancestor with Lake Pend Oreille. This unsampled population was the source of fish in both Medicine-Cave Lakes and Pend Oreille River-Box Canyon Reservoir (Figure 3d).

For all DIYABC analyses, prior parameter estimates were modeled using uniform distribution and default model settings. Samples were collected a t = 0, and time points representing coalescent events in the models were ordered as tc ≥ tb ≥ ta. No time scale was provided for coalescent events at tc, tb, or ta. We assumed a 1:1 sex ratio in our observed dataset. Scenarios were modeled with a generalized stepwise mutation model (Estoup et al. 2002) including all 11 microsatellites with ranges from 0–40 and using default distributions and settings. One sample summary statistics included mean number of alleles, mean gene diversity, and mean size variance for all populations. Two sample summary statistics included Fst for all population pairs. These prior distributions and parameters were used to simulate four million datasets. Posterior probabilities for each scenario were estimated for each dataset using a polychotomous logistic regression on the 1% of simulated datasets with summary statistics closest to the observed dataset. Scenarios were ranked based on their posterior probability estimates. The two scenarios with the highest posterior probability were reanalyzed separately using the same methods and settings as above. This reanalysis with only the top two scenarios allowed us to obtain more refined estimates of confidence in scenarios and reduced computation time. In this second analysis, we simulated 1 million datasets and calculated posterior probabilities as above. To evaluate the potential for these top scenarios and default prior parameters to generate datasets similar to the observed data, we estimated the prior predictive error by simulating 1000 pseudo observed datasets drawing from prior distributions and each scenario equally, following methods outlined by Cornuet et al. (2010). We also calculated Type I and Type II error rates for the scenario with the highest posterior probability by simulating 1000 pseudo observed datasets for the each of the two scenarios, following methods outlined by Cornuet et al. (2010).

Results

We performed 156 tests for departure from Hardy-Weinberg expectations after excluding monomorphic loci within each population. After Bonferroni correction, only one locus in Lake Coeur d'Alene was significant for departure from Hardy-Weinberg equilibrium (corrected p = 0.0003). Excluding monomorphic loci, we performed a total of 698 tests for linkage disequilibrium. After Bonferroni correction, only one test in Lake Roosevelt was significant (corrected p = 0.0007). Based on tests for genetic equilibrium, all data were deemed suitable for subsequent analyses. Estimates of allelic richness were higher for established populations (2.36–3.55) than for populations in recently invaded areas (1.64–2.11; Table 1).

Estimates of pairwise Fst were highly variable among populations. Values were generally higher for comparisons between populations from different

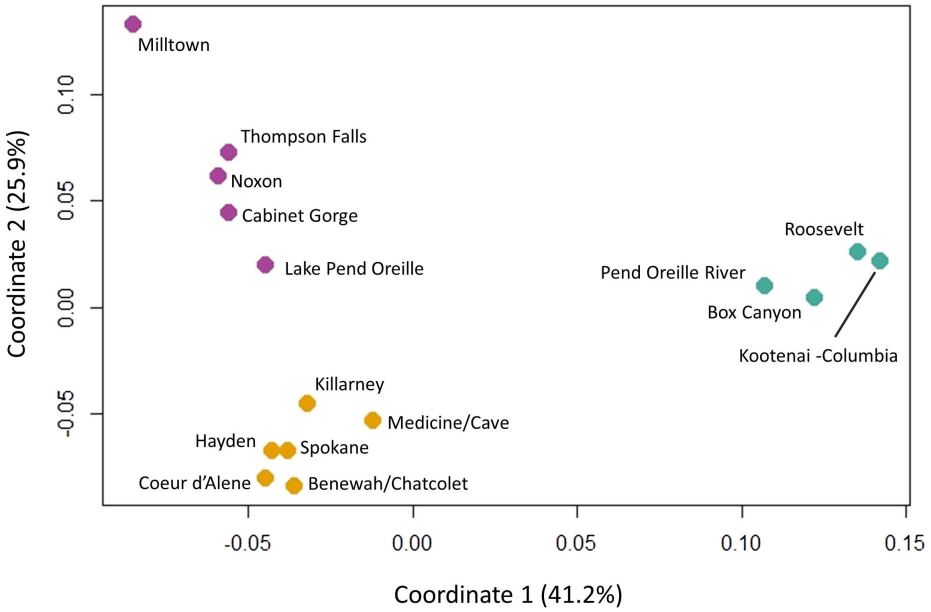

Figure 4. Plot of principle coordinates analysis on northern pike genotype data from populations in the Clark Fork River basin (pink dots), Coeur d'Alene-Spokane River basin (yellow dots) and recently invaded areas in eastern Washington (green dots). The percent of variation explained by coordinates 1 and 2 are shown in axes labels.

basins, as opposed to population comparisons within the same basin (Table S3). For populations in recently invaded areas, Fst values were lower for comparisons within the Coeur d'Alene River basin (average pairwise Fst = 0.292) than the Clark Fork River basin (average pairwise Fst = 0.338). Negative Fst values (i.e., no genetic differentiation) were observed between Medicine and Cave Lakes, and between Lake Benewah and Chatcolet, which supported grouping individuals from these pairs of waterbodies together for subsequent analyses.

Objective 1: Source of northern pike in Eastern Washington Waters

The principal coordinates analysis grouped populations into three major clusters based on river basin of capture (Figure 4). Populations in the Clark Fork River basin grouped most closely with populations immediately up- or downstream. Although it is physically disconnected, Hayden Lake grouped closely with the other populations of the Coeur d'Alene River basin. Populations in recently invaded areas grouped together in a distinct cluster separate from the potential source populations. Together, the first two axes of the principal coordinates analysis explained over 67.1% of the genetic variation observed among populations.

Assignment probabilities of individuals from recently invaded areas to each of the 11 established northern pike populations ranged from 0% to 95.2% (Figure 5, Table S4). For 143 of the 145 fish sampled from recently invaded areas, Medicine-Cave Lakes was the population with the highest assignment probability (Figure 5, Table S4). Individual assignment probabilities to Medicine-Cave Lakes ranged from 0.6 % to 95.2%, with 47

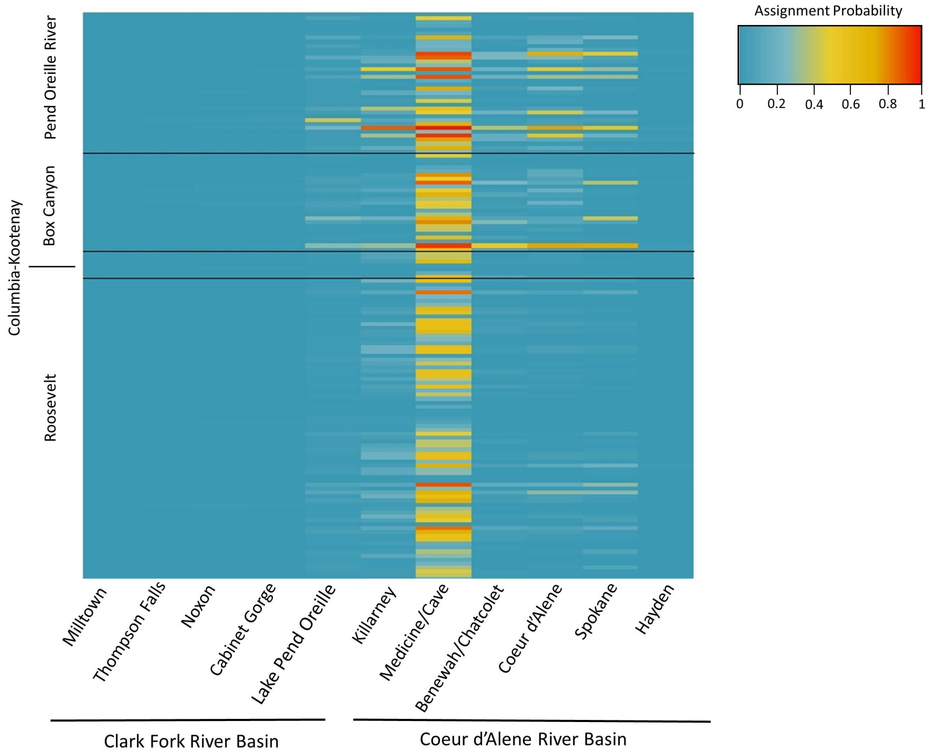

Figure 5. Heat map showing probability of assignment for 145 individuals sampled from recently invaded areas to potential source populations in the Clark Fork and Coeur d'Alene River basins. Recently invaded areas (y-axis) are listed in upstream (top) to downstream (bottom) order. Source populations within each basin (x-axis) are listed in an upstream (left) to downstream (right) order.

individuals assigning with > 50% probability and 13 assigning with > 75% probability. The source population with the highest probability for the remaining two individuals were Lake Pend Oreille (assignment probability = 41.8%) and Lake Coeur d'Alene (assignment probability = 18.4%).

We observed 11 private alleles in the Clark Fork River basin and ten private alleles in the Coeur d'Alene River basin (Table S5). Additionally, we observed one private allele in Lake Roosevelt (EL20-357) but at only 0.6%. One allele (EL20-355) was common in the recently invaded area but was otherwise found only in Medicine/Cave Lake (Coeur d'Alene River basin). All other alleles observed in recently invaded areas were observed in both the Clark Fork and Coeur d'Alene River basins; however, two of these alleles (EL20-337 and B45-206) were common in populations in the recently invaded areas and Coeur d'Alene River basin (frequency ranging from 0.15–0.9) but rare in the Clark Fork River basin (frequency ranging from 0–0.15).

Objective 2: Mechanisms of Expansion at Leading Edge of the Invasion

STRUCTURE results suggest that K = 2 is the most likely number of populations in the recently invaded area. Fish captured in Pend Oreille River and Box Canyon Reservoir belonged to one group (Figure 6). Many fish captured downstream in Columbia River of Canada and in Lake Roosevelt in eastern Washington belonged to a second group of fish, although

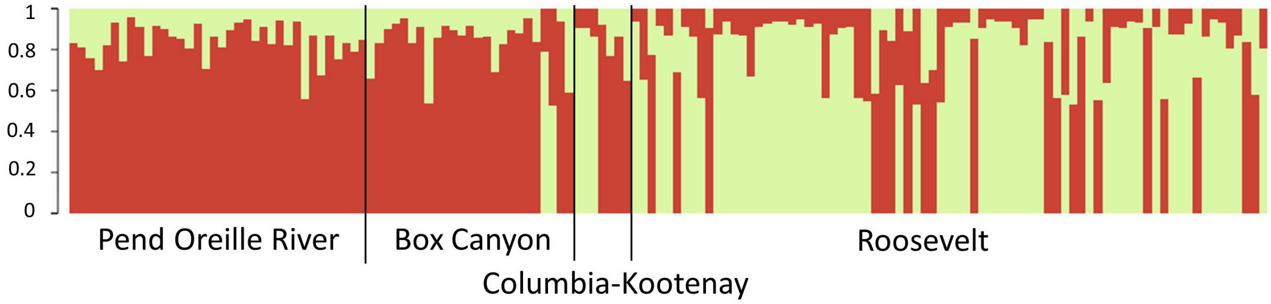

Figure 6. STRUCUTRE plot showing population groupings of northern pike captured in recently invaded waterbodies of eastern Washington based on K = 2 populations. Waterbodies are listed in an upstream to downstream order. Nearly all fish captured upstream of Lake Roosevelt belong to one group (red bars). Most individuals captured in Lake Roosevelt belong to a second group (pale green bars), but individuals belonging to the red group are also present in Lake Roosevelt.

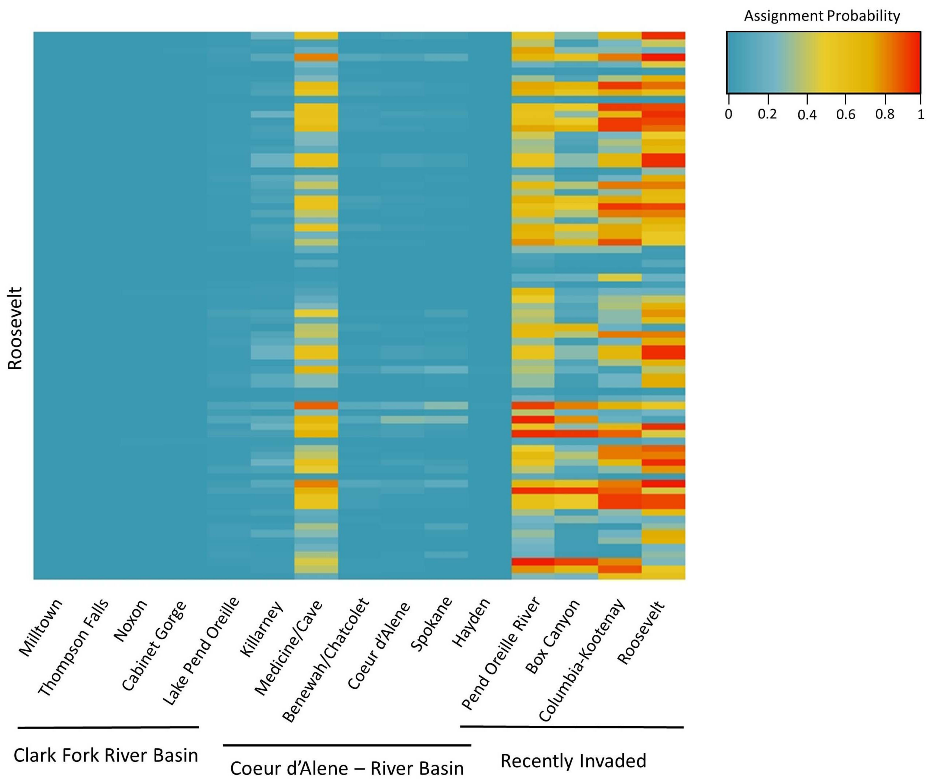

Figure 7. Heat map showing probability of assignment for 77 individuals sampled from Lake Roosevelt to each population sampled in this study. Potential source populations within the Clark Fork River basin, Coeur d'Alene River basin and recently invaded areas are listed in an upstream to downstream order. While many individuals show an elevated assignment probability to Medicine-Cave Lakes (Coeur d'Alene River basin), 71 of the 77 fish had the highest probability of assignment to populations in the recently invaded waterbodies.

fish that grouped with upstream sources were also captured in these downstream waterbodies (Figure 6).

Genetic assignment of fish captured in Lake Roosevelt to all populations in this study (n = 15) ranged from 0% to 99.5% (Figure 7, Table S6). Of the 77 fish captured in Lake Roosevelt, 71 had the highest probability of assignment to self (Lake Roosevelt), or to one of the recently invaded areas upstream. Specifically, of the 71 fish, 35 had the highest probability of assignment to Lake Roosevelt (15.0% to 98.1%), 19 to the Columbia River in Canada (45.8% to 92.4%), three fish to Box Canyon Reservoir (28.1% to

Table 2. Results of DIYABC analysis on scenarios modeling the invasion of northern pike in the Columbia River basin. The first analysis included all four scenarios. The second analysis only included the two scenarios with the highest posterior probability from the first analysis.

	Posterior Probability	95% Confidence Interval
Analysis 1		
Scenario 1	0.324	(0.318 – 0.332)
Scenario 2	0.119	(0.114 – 0.125)
Scenario 3	0.216	(0.210 – 0.222)
Scenario 4	0.340	(0.333 – 0.347)
Analysis 2		
Scenario 1	0.466	(0.456 – 0.476)
Scenario 4	0.534	(0.524 – 0.544)

68.0%), and 14 fish had highest probability of assignment to the Pend Oreille River (probability assignment 1.0% to 97.1%). The remaining six fish had the highest probability of assignment to Medicine-Cave Lakes (0.8% to 68.0%).

Objective 3: Reconstructing the Invasion History

Of the four invasion scenarios compared using DIYABC, Scenarios 1 and 4 had the highest posterior probability estimates (Table 2). In these two scenarios, Medicine-Cave Lakes were either the direct source for fish in the Pend Oreille River and Box Canyon Reservoir (Scenario 1) or shared a common ancestor with these invasive populations (Scenario 4). The posterior probability estimates for Scenarios 2 and 3, both of which modeled a contribution from Lake Pend Oreille, was significantly lower than Scenarios 1 and 4. This suggests that Lake Pend Oreille was not a source population to the Pend Oreille River. In the second analysis comparing only Scenarios 1 and 4, Scenario 4 had the highest posterior probability, although the difference between the two scenarios was small (Table 2). Type I and Type II errors for Scenario 4 were 0.277 and 0.259 respectively. Results of this second analysis demonstrate that our data more closely matches a scenario where Medicine-Cave Lake is not the direct source of northern pike in the Pend Oreille River. Instead, fish in the Pend Oreille River and Medicine-Cave Lakes are related through a common ancestor. The prior predictive error for the analysis with these two models was 0.437, indicating that our ability to obtain our observed data given these scenarios is low.

Discussion

Our results indicate that the recent invasion of northern pike in eastern Washington was not driven by natural dispersal of fish from upstream sources in the Clark Fork River basin of Idaho and Montana. Of all source populations in our study, smaller pairwise Fst values, patterns of allele sharing, and assignment tests all indicate that northern pike in eastern Washington are most closely related to fish in disconnected populations of the Coeur d'Alene River basin of Idaho (Figure 5). Therefore, the initial introduction of northern pike into the Pend Oreille River was most likely the result of human transport. Once established in the Pend Oreille River in eastern Washington State, northern pike spread downstream to the mainstem Columbia River (Figure 4, Table S3). Currently, expansion at the leading edge of the invasion in Lake Roosevelt (a reservoir within the Columbia River) is driven by local reproduction (Figure 7). However, fish from populations upstream in Canada and Washington continue to disperse downstream into Lake Roosevelt (Figure 6).

Low genetic diversity of populations throughout the recently invaded area relative to potential source populations (Table 1) suggests that repeated introductions from populations outside of eastern Washington are not occurring frequently, if at all. Reduced genetic diversity is common in introduced populations, and suppression efforts may create repeated bottlenecks that further reduce genetic diversity in the recently invaded areas over time. However, this effect may be attenuated with repeated dispersal from the source population (Dlugosch and Parker 2008). Repeated introductions from source populations should promote a rapid rebound in diversity and similarity of allele frequencies between source and recipient populations. Under these circumstances, we expect similar levels of allelic richness to source populations (Roman and Darling 2007). We also expect principal coordinates analysis to cluster recently invaded populations with their source population, and low Fst values between source and recipient populations. In contrast, our results show divergence of recently invaded populations from the potential source populations in our dataset (Figure 3).

We must also consider the possibility that the true source population was not sampled in our study. Although northern pike in eastern Washington were most similar to Medicine-Cave Lakes in the Coeur d'Alene River basin, our data do not definitively identify Medicine-Cave Lakes as the source. A comparison in DIYABC showed slightly more support for a scenario in which Medicine-Cave Lakes is related to the true source (Scenario 4), rather than being the true source itself (Scenario 1; Table 2). However, the prior predicative error rates for this analysis indicate that our ability to infer the true invasion history from Scenarios 1 and 4 is limited. Furthermore, the Type I and II error rates indicate that these two scenarios produce relatively similar results. Higher resolution genetic data (i.e., more variable microsatellite markers or a large amount of SNP data) would more clearly distinguish relationships between populations in our dataset. This could reduce error rates, and support modeling of more complex invasion scenarios. Together, this could increase our confidence in the invasion history of northern pike to eastern Washington. Yet, some invasion biologists suggest that information of the true source population and theory underlying "invasiveness" may not be useful for managing established populations (Beaury et al. 2020), or necessary for mounting a rapid response to control a new localized invasion (Simberloff 2003).

The usefulness of identifying source populations depends on the boundaries of the active invasion and scale of suppression efforts. For example, Zelasko et al. (2016) found that removal efforts of northern pike in a subset of invaded portions in the Yampa River led to increased recruitment within the project area and increased immigration of northern pike from upstream sources, negating suppression efforts. They concluded that more comprehensive removal efforts were necessary to effectively control northern pike and protect sensitive native species. Our results demonstrate that fish in the Pend Oreille River are the original source of populations downstream in the Columbia River, with evidence of continued dispersal into Lake Roosevelt. Eradication efforts in Lake Roosevelt would be futile without parallel efforts targeting source populations upstream. Recognizing this need, the Kalispel Tribe of Indians have mounted an aggressive suppression effort throughout the Pend Oreille River in eastern Washington. Over 18,000 northern pike have been removed from the Pend Oreille River since 2012 (Harvey and Bean 2015, 2019, 2020). In Box Canyon Reservoir alone, suppression efforts from 2012 to 2019 reduced catch rates of northern pike by nearly 75% (Harvey and Bean 2020). Similar reductions in northern pike have been observed in the mainstem Columbia River in British Columbia (Canada) following removal efforts from 2014 to 2017 (Doutaz 2019). Removal from these waterbodies immediately upstream of Lake Roosevelt may have slowed expansion at the leading edge of the invasion and increased the likelihood of success for control efforts in Lake Roosevelt.

While state and tribal fisheries managers in Washington State pursue suppression with intent to eradicate northern pike, the ability to suppress established populations of northern pike upstream in Idaho and Montana is limited by both biological and socio-political factors. In the United States, state fish and wildlife agencies are tasked with managing fisheries as a public trust (Organ et al. 2012; Rahel and Taniguchi 2019). In some areas of Montana and Idaho, public interests include recreational fishing for nonnative northern pike. This public interest complicates actions by state agencies to remove established northern pike populations, and meaningful suppression and control of established invasions often requires long-term, extensive resources (Vander Zanden et al. 2010). Additionally, northern pike possess several characteristics associated with the spread and integration of aquatic invasive species, including a long lifespan (16+ years), large adult body size (up to 160 cm) and piscivorous diet with generalist preferences (Marchetti et al. 2004), which may further increase the necessary resources for effective suppression. Even with complete public support, the effort and resources required to fully eradicate northern pike from the upper Columbia River basin may be unattainable and could compromise the ability to address other management and conservation priorities.

For these reasons, and because Lake Pend Oreille (lower Clark Fork River basin) is not currently a source population contributing to the invasion downstream, eradication of northern pike throughout the Clark Fork and Coeur d'Alene River basins is not currently feasible. Instead, managers with the state of Idaho balance conservation objectives, opportunities for recreational fisheries, and current public interests through actions that maintain lower densities of northern pike (e.g., relaxed regulations that promote harvest and removal of northern pike encountered during regular survey work; Idaho Department of Fish and Game 2019), and support tribal biologists pursuing suppression in co-management areas to promote native fisheries (Campbell 2021). This mixed portfolio of management strategies may become increasingly common both direct (e.g., transport of invasive species) and indirect (e.g., climate change) human impacts push ecosystems further from their historic, pristine condition (Aplet and McKinley 2017). Here, the best outcomes may result when management actions are tailored to the resilience and constraints of a particular system.

The northern pike invasion in the Columbia River basin crosses multiple large watersheds as well as state and international boundaries. As a result, the invasion falls under the jurisdiction of multiple federal, state, and tribal natural resource agencies with varying management responsibilities and goals. An understanding of how invasive species, such as northern pike, are spreading provides managers, policy makers, and public outreach coordinators with understanding how their actions affect downstream waterbodies and (in this case) adjacent, but disconnected watersheds. Furthermore, knowledge of source populations will help assess long-term risks and routes of natural and human transport into the future. Extreme climatic events, as well as baseline shifts in climate, habitat, and the ecological community could promote natural dispersal from new source populations (Diez et al. 2012; Estoup and Guillemaud 2010; Havel et al. 2015). Also, the risk of human transport remains wherever northern pike are present. For these reasons, a coordinated and holistic approach to preventing new and repeated dispersal events from these established populations may be necessary (Simpson et al. 2011). Traditional survey methods will allow managers to quantify changes in northern pike densities overtime in established populations and provide information on the risk of new downstream expansion from the Clark Fork River. A better understanding of local population dynamics (such as spatially explicit data on population density and requitement) will inform where and how suppression efforts will be most successful within a given management area or jurisdiction (Green and Grosholz 2021). In addition, emerging monitoring tools, such as environmental DNA, will allow mangers to efficiently monitor for new invasions of northern pike and many other aquatic invasive species (e.g., Carim et al. 2019). If a reintroduction event is detected, a rapid-response plan will minimize risk of new populations or reinvasion in areas where eradication has been successful (e.g., Anderson 2005; Kraus and Duffy 2010). Additionally, the risk of human transport may be reduced through existing monitoring and prevention efforts for other aquatic invasive species. For example, Montana and Idaho implement watercraft inspection programs stations are aimed at reducing transport of aquatic invasive species (Crete et al. 2020; Deleon et al. 2012). While the primary focus is often to reduce unintentional spread of invasive mussels, these check stations make intentional (and illegal) transport of live fish more difficult. Finally, continued public education on the detrimental effects of northern pike invasions on native species (including the most popular game species such as trout; Idaho Department of Fish and Game 2019) may eventually garner more public support for removal efforts.

Ultimately, the benefits of this study are not limited to the introduction and expansion of northern pike in the upper Columbia River basin. DNA profiling is commonly used in wildlife forensics to identify illegal wildlife trade, poaching, or illegal use of wildlife for various forms of human consumption (Signorile et al. 2016; Gouda et al. 2020). Here, DNA samples may be compared to genetic databases for species identification and sources of contraband. Similar approaches can also be used for rapidly identifying the source of new species invasions. For example, results of this study have been used to create a genetic database with genotypes of invasive northern pike in the Columbia River basin. This database has already been used to rule out sources and dispersal routes of northern pike introductions in Washington State waterbodies located outside the Columbia River basin. The ability to rapidly identify source populations of future invasions may help managers prioritize when and where preventative measures such as public outreach and/or targeted suppression will have the greatest benefit.

Acknowledgements

We recognize the people of the Coeur d'Alene, Colville, Kalispel, Kootenai, Okanogan, Salish, and Spokane Tribes, and their lands where this study took place. We thank Shay Wolvert and William Laramie (Colville Confederated Tribes), Jon Firehammer (Coeur d'Alene Tribe of Indians), Nick Bean and Jason Connor (Kalispel Tribe of Indians), Elliot Kittel and Brent Nichols (Spokane Tribe of Indians), Matt Corsi, Ryan Hardy and Nicole Graham (Idaho Department of Fish and Game) and David Schmetterling, Matt Boyer and Ryan Kreiner (Montana Fish, Wildlife and Parks) for their assistance in sample collection. We thank Matt Corsi for his comments on earlier versions of this work. We also thank two anonymous reviewers for their thoughtful suggestions that improved this work.

Funding declaration

Study design, analysis, and interpretation of data was supported USDA Tribal College Research Grant # 2016-38424-25558 which was awarded to authors KJC, LAE, and VD. Additional funding was received form the Colville Confederated Tribes for analysis of additional samples. In kind support from the U.S. Forest Service supported manuscript preparation. In kind support for sample collection was provided by individuals and agencies recognized in the Acknowledgements section.

Authors' contribution

KJC, LAE, HM, and VD contributed to funding acquisition; KJC, LAE, and VD contributed to study design; KJC and LAE contributed to ethics approval, KJC, LMM, and MKS contributed to analysis and interpretation of data; KJC contributed to manuscript writing, and KJC, LAE, LLM, HM, and MKS contributed manuscript review and editing. All authors approved of this manuscript prior to submission.

Ethics and permits

All tissues were handled under tissue use protocol TU004-18LEECS-091918 approved by the University of Montana Institutional Animal Care and Use Committee.

References

Aguilar A, Banks JD, Levine KF, Wayne RK (2005) Population genetics of northern pike (*Esox lucius*) introduced into Lake Davis, California. *Candian Jounral Fisheries and Aquatic Science* 62: 1589–1599, https://doi.org/10.1139/f05-068

Allendorf FW, Luikart G, Aitken SN (2012) Conservation and the genetics of populations. John Wiley and Sons Ltd, Chicester, United Kingdom, 624 pp

Anderson LWJ (2005) California's reaction to *Caulerpa taxifolia*: A model for invasive species rapid response. *Biological Invasions* 7: 1003–1016, https://doi.org/10.1007/s10530-004-3123-z

Aplet GH, McKinley PS (2017) A portfolio approach to managing ecological risks of global change. *Ecosystem Health and Sustainability* 3: e01261, https://doi.org/10.1002/ehs2.1261

Bean NJ, Scholz AT, Connor JM (2011) Diet and growth of Northern Pike (*Esox lucius* Linnaeus, 1758) in Box Canyon Reservoir, Pend Oreille River, Washington. Bonneville Power Administration Proejct # 1977-004-00, https://www.cbfish.org/Document.mvc/Viewer/P123897

Beaury EM, Fusco EJ, Jackson MR, Laginhas BB, Morelli TL, Allen JM, Pasquarella VJ, Bradley BA (2020) Incorporating climate change into invasive species management: insights from managers. *Biological Invasions* 22: 233–252, https://doi.org/10.1007/s10530-019-02087-6

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26: 333–339, https://doi.org/10.1016/j.tree.2011.03.023

Britton JR, Gozlan RE, Copp GH (2011) Managing non-native fish in the environment. *Fish and Fisheries* 12: 256–274, https://doi.org/10.1111/j.1467-2979.2010.00390.x

Cabrera AA, Palsbøll PJ (2017) Inferring past demographic changes from contemporary genetic data: A simulation-based evaluation of the ABC methods implemented in DIYABC. *Molecular Ecology Resources* 17: e94–e110, https://doi.org/10.1111/1755-0998.12696

Campbell K (2021) Pike removal to continue in sections of Lake Coeur d'Alene. Idaho Fish and Game, Coeur d'Alene, ID, https://idfg.idaho.gov/press/pike-removal-continue-sections-lake-coeur-dalene-0 (accessed 10 May 2021)

Carim KJ, Caleb Dysthe J, McLellan H, Young MK, McKelvey KS, Schwartz MK (2019) Using environmental DNA sampling to monitor the invasion of nonnative *Esox lucius* (northern pike) in the Columbia River basin, USA. *Enviornmental DNA* 1: 215–226, https://doi.org/10.1002/edn3.22

Cornuet J-M, Piry S, Luikart G, Estoup A, Solignac M (1999) New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics* 153: 1989–2000, https://doi.org/10.1093/genetics/153.4.1989

Cornuet J-M, Ravigné V, Estoup A (2010) Inference on population history and model checking using DNA sequence and microsatellite data with the software DIYABC (v1. 0). *BMC Bioinformatics* 11: 401, https://doi.org/10.1186/1471-2105-11-401

Cornuet J-M, Pudlo P, Veyssier J, Dehne-Garcia A, Gautier M, Leblois R, Marin J-M, Estoup A (2014) DIYABC v2.0: a software to make approximate Bayesian computation inferences about population history using single nucleotide polymorphism, DNA sequence and microsatellite data. *Bioinformatics* 30: 1187–1189, https://doi.org/10.1093/bioinformatics/btt763

Craig JF (2008) A short review of pike ecology. *Hydrobiologia* 601: 5–16, https://doi.org/10.1007/s10750-007-9262-3

Crete Z, Gudel J, Woolf T (2020) Aquatic Invasive Species Prevention Program - Watercraft Inspection Report. Montana Fish, Wildlife, and Parks, Helena, MT, 23 pp

Cristescu ME (2015) Genetic reconstructions of invasion history. *Molecular Ecology* 24: 2212–2225, https://doi.org/10.1111/mec.13117

Deleon R, Ferriter A, Haller WT, Hosler DM, Layne CR, McMahon RF, Stubbs D, Woolf T (2012) A review of the state of Idaho Dreissenid mussel prevention and contingency plans. http://aquatics.org/musselreport.pdf

Diez JM, D'Antonio CM, Dukes JS, Grosholz ED, Olden JD, Sorte, CJB, Blumenthal DM, Bradley BA, Early R, Ibáñez I, Jones SJ, Lawler JJ, Miller LP (2012) Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment* 10: 249–257, https://doi.org/10.1890/110137

Dlugosch KM, Parker IM (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology* 17: 431–449, https://doi.org/10.1111/j.1365-294X.2007.03538.x

Doutaz DJ (2019) Columbia River Northern Pike: Investigating the Ecology of British Columbia's New Apex Invasive Freshwater Predator. Master's Thesis. Thompson Rivers University, 79 pp

Dunker K, Sepulveda A, Massengill R, Rutz D (2018) The northern pike, a prized native but disastrous invasive. In: Nilsson A, Skov C (eds), Biology and Ecology of Pike, CRC Press pp 356–398, https://doi.org/10.1201/9781315119076-17

Epanchin-Niell RS, Hastings A (2010) Controlling established invaders: integrating economics and spread dynamics to determine optimal management. *Ecology Letters* 13: 528–541, https://doi.org/10.1111/j.1461-0248.2010.01440.x

Estoup A, Guillemaud T (2010) Reconstructing routes of invasion using genetic data: why, how and so what? *Molecular Ecology* 19: 4113–4130, https://doi.org/10.1111/j.1365-294X.2010.04773.x

Estoup A, Jarne P, Cornuet JM (2002) Homoplasy and mutation model at microsatellite loci and their consequences for population genetics analysis. *Molecular Ecology* 11: 1591–1604, https://doi.org/10.1046/j.1365-294X.2002.01576.x

Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* 10: 564–567, https://doi.org/10.1111/j.1755-0998.2010.02847.x

Firehammer JA, Vitale AJ (2020) Implementation of Fisheries Enhancement Opportunities on the Coeur d'Alene Reservation: Research, Monitoring, and Evaluation Report, 1/1/2018 - 12/31/2019 Annual Report. Project #1990-044-00. https://www.cdatribe-nsn.gov/nr/wp-content/uploads/sites/5/2020/01/CDA-RME-18-19.pdf

Gouda S, Kerry RG, Das A, Chauhan NS (2020) Wildlife forensics: A boon for species identification and conservation implications. *Forensic Science International* 317: 110530, https://doi.org/10.1016/j.forsciint.2020.110530

Great Falls Tribune (1986) Pike infest western Montana Great Falls, MT, February 5, 1986

Green SJ, Grosholz ED (2021) Functional eradication as a framework for invasive species control. *Frontiers in Ecology and the Environment* 19: 98–107, https://doi.org/10.1002/fee.2277

Hammer D, Hughes R (2011) Removing a Dam, Restoring a River: The Story of Milltown, Montana. Paper presented at the American Fisheries Society 141st Meeting, Seattle, WA, September 2011

Handley LJL, Estoup A, Evans DM, Thomas CE, Lombaert E, Facon B, Aebi A, Roy HE (2011) Ecological genetics of invasive alien species. *Biocontrol* 56: 409–428, https://doi.org/10.1007/s10526-011-9386-2

Harvey S, Bean N (2015) Kalispel non-native fish suppression project 2014 Annual Report, Kalispel Tribe of Indians, Bonneville Power Administration Project # 2007-149-00. https://www.cbfish.org/Document.mvc/Viewer/P143748

Harvey S, Bean N (2019) Kalipel Non-native Fish Supression Project 2018 Annual Report, Bonneville Power Administration Project # 2007-149-00. https://www.cbfish.org/Document.mvc/Viewer/P165092

Harvey S, Bean N (2020) Kalispel Non-native Fish Suppression project- 2019 Annual Report, Bonneville Power Administration Project # 2007-149-00. https://www.cbfish.org/Document.mvc/Viewer/P172302

Havel JE, Kovalenko KE, Thomaz SM, Amalfitano S, Kats LB (2015) Aquatic invasive species: challenges for the future. *Hydrobiologia* 750: 147–170, https://doi.org/10.1007/s10750-014-2166-0

He X, Kitchell JF (1990) Direct and indirect effects of predation on a fish community: A whole-lake experiment. *Transactions of the American Fisheries Society* 119: 825–835, https://doi.org/10.1577/1548-8659(1990)119<0825:DAIEOP>2.3.CO;2

Idaho Department of Fish and Game (2019) Fisheries management plan 2019-2024. Idaho Department of Fish and Game, Boise, ID, 388 pp

Jackson MC, Grey J (2013) Accelerating rates of freshwater invasions in the catchment of the River Thames. *Biological Invasions* 15: 945–951, https://doi.org/10.1007/s10530-012-0343-5

Kalinowski ST (2005) hp-rare 1.0: a computer program for performing rarefaction on measures of allelic richness. *Molecular Ecology Notes* 5: 187–189, https://doi.org/10.1111/j.1471-8286.2004.00845.x

Kimura M, Weiss GH (1964) The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics* 49: 561, https://doi.org/10.1093/genetics/49.4.561

Kraus F, Duffy DC (2010) A successful model from Hawaii for rapid response to invasive species. *Journal for Nature Conservation* 18: 135–141, https://doi.org/10.1016/j.jnc.2009.07.001

Lee CD, Parsons T (2020) Lake Roosevelt Northern Pike Suppression and Monitoring 2019 Annual Report, Bonneville Power Administraion Project #2017-004-00, Chapter 1. https://www.cbfish.org/Document.mvc/Viewer/P172596

Lee C, Pavlik-Kunkel D, Miller A, Scofield B, Walther B, Knudson T (2010) Lake Roosevelt Fisheries Evaluation Report. Spokane Tribe of Indians, Bonneville Power Administration Projet # 1994-043-00. https://www.cbfish.org/Document.mvc/Viewer/P117257

Marchetti MP, Moyle PB, Levine R (2004) Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology* 49: 646–661, https://doi.org/10.1111/j.1365-2427.2004.01202.x

McLellan HJ, Wolvert S, Kittel EC, Silver AO, Lee C (2018) Lake Roosevelt Northern Pike Suppression and Monitoring, 2017 Annual Report, Bonneville Power Administration Project # 1994-043-00. https://www.cbfish.org/Document.mvc/Viewer/P165005

McLellan HJ, Wolvert S, Silver AO, Thurman KT, Lee CD, Parsons T (2019) Lake Roosevelt Northern Pike Suppression and Monitoring, 2018 Annual Report, Bonneville Power Administration Project # 1994-043-00 and 2017-004-00. https://www.cbfish.org/Document.mvc/Viewer/P165005

McMahon TE, Bennett DH (1996) Walleye and Northern Pike. *Fisheries* 21: 6–13, https://doi.org/10.1577/1548-8446(1996)021<0006:WANP>2.0.CO;2

Miller LM, Kapuscinski AR (1997) Historical analysis of genetic variation reveals low effective population size in a northern pike (*Esox lucius*) population. *Genetics* 147: 1249–1258, https://doi.org/10.1093/genetics/147.3.1249

Muhfled CC, Bennett DH, Steinhorst RK, Marotz B, Boyer MC (2008) Using bioenergetics modeling to estimate consumptions of native juvenile salmonids by nonnative northern pike in the Upper Flathead River System, Montana. *North American Journal of Fisheries Management* 28: 636–648, https://doi.org/10.1577/M07-004.1

National Marine Fisheries Service (2016) Endangered and threatened species; 5-year reviews for 28 listed species of Pacific salmon, steelhead, and eulachon. *Federal Registry* 81: 33468–33469

Organ JF, Geist V, Mahoney SP, Williams S, Krausman PR, Batcheller GR, Decker TA, Carmichael R, Nanjappa P, Regan R (2012) The North American model of wildlife conservation. The Wildlife Society Technical Review 12-04 The Wildlife Society Bethseda, Maryland, 49 pp

Ostovar K (2012) Recolonization of fish in the Telegraph Creek basin: An assessment of barrier removals and habitat improvements. Rocky Mountain College. American Prairie Reserve. https://www.americanprairie.org/sites/default/files/APR-Fish-Report-2012.pdf

Ouellet-Cauchon G, Normandeau E, Mingelbier M, Bernatchez L (2014) EST-based microsatellites for northern pike (*Esox lucius*) and cross-amplification across all *Esox* species. *Conservation Genetic Resources* 6: 451–454, https://doi.org/10.1007/s12686-013-0123-2

Paetkau D, Calvert W, Stirling I, Strobeck C (1995) Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4: 347–354, https://doi.org/10.1111/j.1365-294X.1995.tb00227.x

Paetkau D, Slade R, Burden M, Estoup A (2004) Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Molecular Ecology* 13: 55–65, https://doi.org/10.1046/j.1365-294X.2004.02008.x

Page LM, Burr BM (2011) A field guide to freshwater fishes of North America north of Mexico. Second Edition. Houghton Mifflin Harcourt, New York, New York, 688 pp

Peakall R, Smouse PE (2006) Genalex 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6: 288–295, https://doi.org/10.1111/j.1471-8286.2005.01155.x

Peakall R, Smouse PE (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. *Bioinformatics* 28: 2537–2539, https://doi.org/10.1093/bioinformatics/bts460

Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A (2004) GENECLASS2: A software for genetic assignment and first-generation migrant detection. *Journal of Heredity* 95: 536–539, https://doi.org/10.1093/jhered/esh074

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics* 155: 945–959, https://doi.org/10.1093/genetics/155.2.945

Rahel FJ (2000) Homogenization of fish faunas across the United States. *Science* 288: 854–856, https://doi.org/10.1126/science.288.5467.854

Rahel FJ, Taniguchi Y (2019) A comparison of freshwater fisheries management in the USA and Japan. *Fisheries Science* 85: 271–283, https://doi.org/10.1007/s12562-019-01291-6

Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences* 94: 9197–9201, https://doi.org/10.1073/pnas.94.17.9197

Raymond M, Rousset F (1995) GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86: 248–249, https://doi.org/10.1093/oxfordjournals.jhered.a111573

Ricciardi A (2006) Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions* 12: 425–433, https://doi.org/10.1111/j.1366-9516.2006.00262.x

Ricciardi A, Blackburn TM, Carlton JT, Dick JTA, Hulme PE, Iacarella JC, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ, Pyšek P, Richardson DM, Ruiz GM, Simberloff D, Sutherland WJ, Wardle DA. Aldridge DC (2017) Invasion science: a horizon scan of emerging challenges and opportunities. *Trends in Ecology and Evolution* 32: 464–474, https://doi.org/10.1016/j.tree.2017.03.007

Roman J, Darling JA (2007) Paradox lost: genetic diversity and the success of aquatic invasions. *Trends in Ecology and Evolution* 22: 454–464, https://doi.org/10.1016/j.tree.2007.07.002

Rousset F (2008) Genepop'007: a complete reimplimentation of the Genepop software for Windows and Linux. *Molecular Ecology Recources* 8: 103–106, https://doi.org/10.1111/j.1471-8286.2007.01931.x

Sanderson BL, Barnas KA, Rub AMW (2009) Nonindigenous species of the Pacific Northwest: an overlooked risk to endangered salmon? *BioScience* 59: 245–256, https://doi.org/10.1525/bio.2009.59.3.9

Schmetterling DA, Clark R, Elam T (2015) Scale and permanence: Monitoring removal of Milltown Dam, 1998-2014. Paper presented at the Clark Fork Symposium, Missoula, MT, April 24, 2015

Sepulveda AJ, Rutz DS, Ivery SS, Dunker KJ, Gross JA (2013) Introduced northern pike predation on salmonids in southcentral Alaska. *Ecology of Freshwater Fish* 2: 268–279, https://doi.org/10.1111/eff.12024

Sepulveda AJ, Rutz DS, Dupuis AW, Shields PA, Dunker KJ (2015) Introduced northern pike consumption of salmonids in southcentral Alaska. *Ecology of Freshwater Fish* 24: 519–531, https://doi.org/10.1111/eff.12164

Signorile AL, Reuman DC, Lurz PWW, Bertolino S, Carbone C, Wang J (2016) Using DNA profiling to investigate human-mediated translocations of an invasive species. *Biological Conservation* 195: 97–105, https://doi.org/10.1016/j.biocon.2015.12.026

Simberloff D (2003) How much information on Population Biology Is Needed to Manage Introduced Species? *Conservation Biology* 17: 83–92, https://doi.org/10.1046/j.1523-1739.2003.02028.x

Simpson A, Jarnevich C, Madsen J, Westbrooks R, Fournier C, Mehrhoff L, Browne M, Graham J, Sellers (2009) Invasive species information networks: collaboration at multiple scales for prevention, early detection, and rapid response to invasive alien species. *Biodiversity* 10: 5–13, https://doi.org/10.1080/14888386.2009.9712839

Slatkin M, Excoffier L (2012) Serial Founder Effects During Range Expansion: A Spatial Analog of Genetic Drift. *Genetics* 191: 171–181, https://doi.org/10.1534/genetics.112.139022

Slatkin M, Maddison WP (1990) Detecting isolation by distance using phylogenies of genes. *Genetics* 126: 249–260, https://doi.org/10.1093/genetics/126.1.249

Sol SY, Lomax DP, Hanson AC, Corbett C, Johnson LL (2021) Fish Communities in the Tidal Freshwater Wetlands of the Lower Columbia River. *Northwest Science* 94: 208–230, 223, https://doi.org/10.3955/046.094.0301

Strayer DL, Dudgeon D (2010) Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society* 29: 344–358, https://doi.org/10.1899/08-171.1

Vander Zanden MJ, Hansen GJ, Higgins SN, Kornis MS (2010) A pound of prevention, plus a pound of cure: early detection and eradication of invasive species in the Laurentian Great Lakes. *Journal of Great Lakes Research* 36: 199–205, https://doi.org/10.1016/j.jglr.2009.11.002

Watkins C, Ryan R, Fredericks J, Yallaly K, Bouwens K, Kaus D, Cux A (2019) Idaho Department of Fish and Game Fishery Management Annual Reprot - Pandhandle Region 2014. Idaho Fish and Game Report No. 18-101, 205 pp

Zelasko KA, Bestgen KR, Hawkins JA, White GC (2016) Evaluation of a long-term predator removal program: abundance and population dynamics of invasive Northern Pike in the Yampa River, Colorado. *Transactions of the American Fisheries Society* 145: 1153–1170, https://doi.org/10.1080/00028487.2016.1173586

Supplementary material

The following supplementary material is available for this article:

Table S1. Primer sequences , dyes, source and multiplex combinations for PCR amplification of northern pike DNA.
Table S2. Primer master mix recipes for each PCR mutliplex.
Table S3. Estimates of pairwise Fst values among all populations in this dataset.
Table S4. Probability of assignment for northern pike from recently invaded areas in eastern Washington to established populations in the Clark Fork and Coeur d'Alene-Spokane River basins.
Table S5. Microsatellite allele frequencies by population.
Table S6. Probability of assignment for northern pike from Lake Roosevelt to potential source populations, including populations in the Clark Fork and Coeur d'Alene River basins, as well as populations in recently invaded areas of eastern Washington.

This material is available as part of online article from:
http://www.reabic.net/journals/mbi/2022/Supplements/MBI_2022_Carim_etal_SupplementaryTables.xlsx