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Broad-scale eDNA sampling for describing aquatic species distributions in running waters: Pacific lamprey *Entosphenus tridentatus* in the upper Snake River, USA

Michael K. Young[1] | Daniel J. Isaak[2] | David Nagel[2] | Dona L. Horan[2] | Kellie J. Carim[3] | Thomas W. Franklin[1] | Victoria A. Zeller[1] | Brett Roper[4] | Michael K. Schwartz[1]

[1]USDA Forest Service, Rocky Mountain Research Station, National Genomics Center for Wildlife and Fish Conservation, Missoula, Montana, USA

[2]USDA Forest Service, Rocky Mountain Research Station, Boise Spatial Streams Group, Boise, Idaho, USA

[3]USDA Forest Service, Rocky Mountain Research Station, Aldo Leopold Wilderness Research Institute, Missoula, Montana, USA

[4]USDA Forest Service, National Stream and Aquatic Ecology Center, Logan, Utah, USA

Correspondence
USDA Forest Service, Rocky Mountain Research Station, National Genomics Center for Wildlife and Fish Conservation, 800 East Beckwith Avenue, Missoula, Montana 59802, USA.
Email: michael.k.young@usda.gov

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Abstract

One of the most fundamental yet challenging tasks for aquatic ecologists is to precisely delineate the range of species, particularly those that are broadly distributed, require specialized sampling methods, and may be simultaneously declining and increasing in different portions of their range. An exemplar is the Pacific lamprey *Entosphenus tridentatus*, a jawless anadromous fish of conservation concern that is actively managed in many coastal basins in western North America. To efficiently determine its distribution across the accessible 56,168 km of the upper Snake River basin in the north-western United States, we first delimited potential habitat by using predictions from a species distribution model based on conventionally collected historical data and from the distribution of a potential surrogate, Chinook salmon *Oncorhynchus tshawytscha*, which yielded a potential habitat network of 10,615 km. Within this area, we conducted a two-stage environmental DNA survey involving 394 new samples and 187 archived samples collected by professional biologists and citizen scientists using a single, standardized method from 2015 to 2021. We estimated that Pacific lamprey occupied 1875 km of lotic habitat in this basin, of which 1444 km may have been influenced by recent translocation efforts. Pacific lamprey DNA was consistently present throughout most river main stems, although detections became weaker or less frequent in the largest and warmest downstream channels and near their headwater extent. Pacific lamprey were detected in nearly all stocked tributaries, but there was no evidence of indigenous populations in such habitats. There was evidence of post-stocking movement because detections were 1.8–36.0 km upstream from release sites. By crafting a model-driven spatial sampling template and executing an eDNA-based sampling campaign led by professionals and volunteers, supplemented by previously collected samples, we established a benchmark for understanding the current range of Pacific lamprey across a large portion of its range in the interior Columbia River basin. This approach could be tailored to refine range estimates for other wide-ranging aquatic species of conservation concern.

KEYWORDS
biobank, crowd-sourcing, eDNA, pacific northwest, range estimation, snake river, species distribution model

1 | INTRODUCTION

To an ecologist, perhaps the most fundamental property of a taxon is its distribution (Hortal *et al*., 2015). For most aquatic taxa, however, characterizing distributions is problematic because estimating habitat occupancy is often imprecise, time-consuming or difficult to implement at the spatial and temporal scales sufficient to understand a species' status. A consequence is that broad-scale surveys often rely on single samples from readily accessible points on a subsample of potentially occupied streams at the expense of more comprehensive inventories throughout a species' range (Kadmon *et al*., 2004). That many forms of conventional sampling require permits from regulatory agencies and biologists with extensive experience and specialized skills can further limit the extent and timeliness of species distribution sampling (Clemens *et al*., 2022). An additional complication is that an actively managed species of conservation concern may be declining in some areas and expanding in others. Collectively, these issues often lead to relatively haphazard sampling of potential or occupied habitats using a variety of methods in times or places that are convenient, lending a biased and fragmented perspective about the distribution of a species over time (Anderson, 2001). This is often coupled with a taxonomic bias because the material and human investments associated with broad-scale sampling are generally reserved for high-profile species at the expense of monitoring less charismatic ones that may merit conservation action.

Methods based on environmental DNA (eDNA) sampling can overcome many of these issues. The relatively limited equipment and streamlined protocols associated with some forms of eDNA sampling (*e.g*., Carim *et al*., 2016), when coupled with standardized field and laboratory approaches, often produce higher site-level detection probabilities for eDNA sampling relative to conventional methods for aquatic species (Itakura *et al*., 2019; Jerde *et al*., 2011; Wilcox *et al*., 2016). These in turn can yield robust estimates of local habitat occupancy across large portions or all of a species range, especially if the workforce can be bolstered by the participation of citizen scientists (Biggs *et al*., 2018; Isaak *et al*., 2018a). Nonetheless, the costs of eDNA sampling, while generally less than those of conventional methods (Lugg *et al*., 2018; Wilcox *et al*., 2016), are not trivial. Hence, a critical component of an eDNA sampling campaign is to focus on potential habitat, for example by disproportionately sampling locations with nonzero occupancy probabilities based on predictions from species distribution models (Guisan *et al*., 2006; Rubenson & Olden, 2020). Doing so in a regularized fashion across fluvial networks can leverage the high detection rates from eDNA sampling to precisely and efficiently delineate species distributions. That efficiency can be heightened by the availability of an archive of previously collected samples that can supplement new samples for addressing questions about the current or changing distribution of species (Dysthe *et al*., 2018; Franklin *et al*., 2019; Jarman *et al*., 2018).

An exemplar of the many issues associated with monitoring of species of conservation concern is the Pacific lamprey *Entosphenus tridentatus* (Richardson, 1836), a jawless, anadromous fish native to the Pacific Rim from Japan to Baja California. In western North America, this species was once so abundant as to be occasionally regarded as a nuisance: the mass die-off of adults following spawning forced Indigenous peoples to temporarily rely on alternative sources for clean water (Petersen-Lewis, 2009), and even fisheries biologists late in the 20th century mentioned removing 1000s of immature specimens trapped on irrigation structures (Virgil Moore, Idaho Department of Fish and Game, personal communication). Like many anadromous species in the region, however, Pacific lamprey have markedly declined in recent decades (Clemens *et al*., 2021) and were petitioned for listing under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 2004). These declines were especially pronounced in the interior Columbia River basin in the north-western United States, which hosts populations that undertake the longest freshwater migration of any species of lamprey (~1200 km; Renaud, 2011) and where counts of adults migrating upstream have decreased by more than an order of magnitude concomitant with contractions in the extent of larval habitat occupancy over the last few decades (IDFG, 2011; Fish Passage Center, https://www.fpc.org/webapps/adultsalmon/Q_adultcounts_lamprey_dataquery.php).

In response to the repeated calls for better information on the distribution of Pacific lamprey (Clemens *et al*., 2017; Luzier *et al*., 2011; Reid & Goodman, 2015), methods have been developed to target particular habitats and life stages (*e.g*., larval forms in wadeable streams (Dunham *et al*., 2013) or their deep-water mouths (Harris & Jolley, 2017)). These have been supplemented by seasonal counts at index sites originally chosen for monitoring other species [*e.g*., screw traps for capturing outmigrating salmon smolts in road-accessible streams (Hayes *et al*., 2013) or redd counts in reaches chosen for monitoring steelhead *O. mykiss* spawning (Clemens *et al*., 2021)]. Although these techniques can be effective for determining the presence of Pacific lamprey (Mayfield *et al*., 2014; Reid & Goodman, 2015, 2016; Harris *et al*., 2016), index sites or reaches are uninformative for determining the upstream extent of occupied habitat, whereas the labour-intensive sampling required to describe larval habitat occupancy (Harris *et al*., 2020) precludes its broad-scale application. However, precise yet broad-scale monitoring of Pacific lamprey is critical to assessing whether declines are continuing in some headwater tributaries (IDFG, 2011) and to gauge the success of adult translocations in others (Ward *et al*., 2012).

Whole-basin assessments of Pacific lamprey distributions derived from eDNA sampling represent a potential solution. Because site-level detection rates of Pacific lamprey with eDNA sampling can approach 1.0 (Ostberg *et al*., 2019), the method can reliably determine their presence (Carim *et al*., 2017; Ostberg *et al*., 2018) and extent in small river basins (Duda *et al*., 2021). Furthermore, using predictions from a species distribution model to refine eDNA sampling surveys has

proven successful for other taxa. Rubenson and Olden (2020), for example, aggregated historical occurrence records for invasive smallmouth bass *Micropterus dolomieu* (Lacepède, 1802) in the interior Columbia River basin in west-central North America, modelled its distribution and then collected eDNA samples in river reaches along the invasion front to ascertain the extent of upstream range expansion. Riaz *et al*. (2020) recalibrated an initial species distribution model with newly collected eDNA sampling data, which led to the discovery of new populations of the target species. Young *et al*. (2017) used a model to identify potential natal habitat for juvenile bull trout *Salvelinus confluentus* (Suckley, 1859) in the U.S. Pacific Northwest (Isaak *et al*., 2015) that guided eDNA sampling surveys (https://www.fs.fed.us/rm/boise/AWAE/projects/BullTrout_eDNA.html) that helped resolve uncertainties about the distribution and ecology of that species (Isaak *et al*., 2022; Wilcox *et al*., 2018).

Here, we adopted a similar approach by developing a species distribution model for Pacific lamprey in the >50,000 km upper Snake River basin, the largest tributary of the Columbia River, based on occupancy data collected using an array of conventional methods. We then crafted a spatial sampling template for all potentially occupied habitats by selecting sampling locations based on their occupancy probabilities, supplemented by locations in streams with translocations or that were used for spawning by anadromous salmonids. We then completed this sampling by relying on a combination of professionals and volunteers, supplemented with samples from a regional archive already collected as part of other eDNA-based species surveys (Young *et al*., 2018). Finally, in several accessible occupied basins we undertook a second, more spatially intensive survey to precisely delineate the headwater extent of Pacific lamprey and estimate their present distribution.

2 | MATERIALS AND METHODS

2.1 | Ethical statement

No ethical approval or collection permits were required because no animals were collected as part of this study.

2.2 | Study area and focal species

Pacific lamprey in the interior Columbia River basin exhibit a complex life history that may take well over a decade to complete (Clemens *et al*., 2017; Hess *et al*., 2022). All known populations are anadromous and consist of relatively large-bodied, stream-maturing adults (Hess *et al*., 2014; Parker *et al*., 2019) that spawn in late spring to early summer in low-gradient streams or rivers, often in locations that also host spawning populations of Pacific salmon and steelhead (*Oncorhynchus* spp.; Gunckel *et al*., 2009; Wallace & Zaroban, 2013). After a brief period of incubation, the blind larvae emerge from the spawning sites and become benthic, detrital filter-feeders that occupy depositional habitats for 3–8 years, occasionally relocating downstream (often during floods; Moser *et al*., 2015). After reaching some threshold size (often specific to a particular basin; Manzon *et al*., 2015), individuals acquire functional eyes and rasping mouthparts, and in autumn begin a months-long migration to the ocean. Once there, they attach to other fish to feed on blood and surface flesh for an additional 2–4 years, then cease feeding and return to freshwater to mature and spawn. By early autumn, adults often reach overwintering habitats in larger rivers (in our study area, near the junction of the Clearwater and Snake Rivers; McIlraith *et al*., 2015) downstream from their eventual spawning locations.

We focused on the 76,617 km^2 portion of the Snake River basin upstream from the mouth of the Clearwater River, which includes 56,168 km of streams currently accessible to Pacific lamprey in Idaho and portions of north-eastern Oregon and south-eastern Washington (Figures 1 and 2). The topography within this area is mountainous, the climate is characterized by cold, wet winters with moderate to heavy snow accumulations at high elevations, and stream hydrographs are driven by snowmelt runoff. Most of the land surface is publicly owned (81%) and federally administered, although there are substantial private lands in most stream and river valleys. In some historically accessible portions of the basin, Pacific lamprey were extirpated by dams lacking passage for migratory fish – the Dworshak Dam on the North Fork Clearwater River and the Hells Canyon Dam on the main-stem Snake River – and by smaller water development structures in other locations. The Lewiston Dam on the lower Clearwater River (removed in 1972) and the Harpster Dam on the South Fork Clearwater River (removed in 1963) also precluded or reduced upstream access prior to their removal, but lamprey remained or recolonized upstream of both former dam sites (IDFG, 2011). Similar structures blocking access to historically occupied habitat on the Lemhi River and upper Salmon River have also been removed in the last few decades, but there has been no evidence of recolonization (IDFG, 2011). In Idaho, recent sampling indicated that indigenous populations of Pacific lamprey remained in the Snake, Salmon and Clearwater Rivers (IDFG, 2011; McIlraith *et al*., 2015; Hess *et al*., 2022), and in Oregon and Washington wild populations were believed to be present in the Imnaha and Grande Ronde Rivers (U.S. Fish and Wildlife Service, 2004). Since 2007, tribal biologists have been attempting to restore Pacific lamprey to certain areas by capturing maturing adults at main-stem Columbia River dams and overwintering them in hatcheries (Ward *et al*., 2012). In early summer, most adults are released in headwater tributaries or upper river main stems, where traditional ecological knowledge affirmed their historical presence (Tod Sween, Nez Perce Tribe, and Aaron Jackson, Confederated Tribes of the Umatilla Indian Reservation, personal communications). These adults presumably spawn shortly thereafter, although seasonal access issues occasionally led to stocking at other times, and some adults may have overwintered and spawned the following year (Hess *et al*., 2022).

2.3 | Stream network and species distribution model

Because larval forms periodically drift downstream throughout their freshwater phase, we hypothesized that all areas downstream from

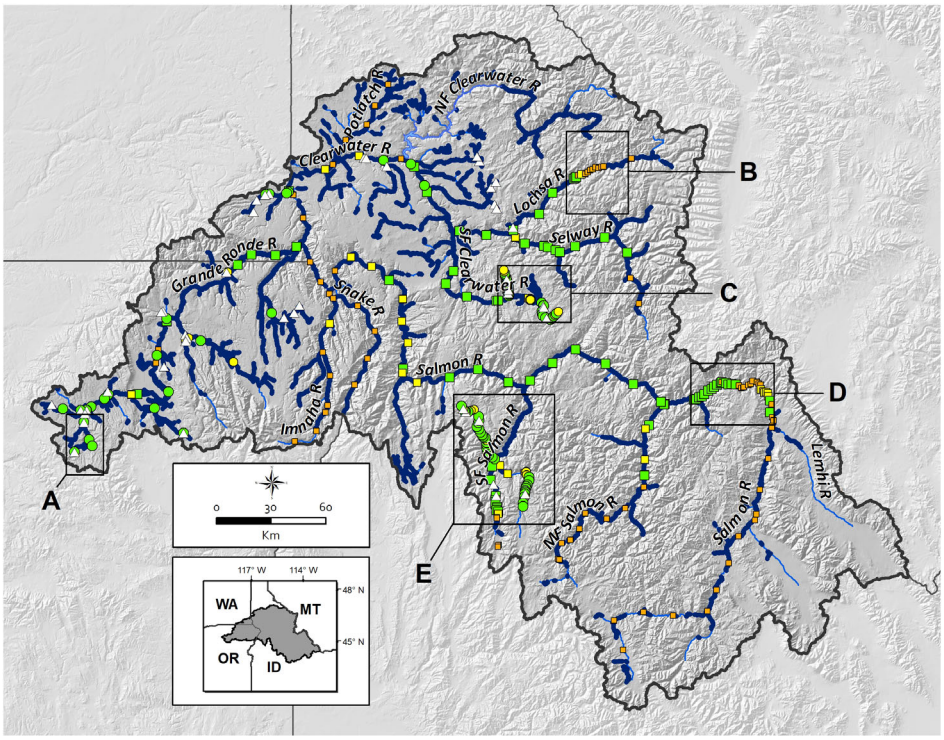

FIGURE 1 Environmental DNA sampling locations (squares, main-stem sites; circles, tributary sites) and translocation sites (white triangles) in the upper Snake River basin, Idaho-Oregon-Washington. Sample marker colour denotes the number of triplicate wells that were positive for Pacific lamprey DNA (orange, 0 wells; yellow, 1–2 wells; green, 3 wells) in the laboratory analyses. Heavy blue lines denote portions of the network predicted by the species distribution model to have a probability of occupancy >0.1. Inset boxes A–E are enlarged in Figure 2

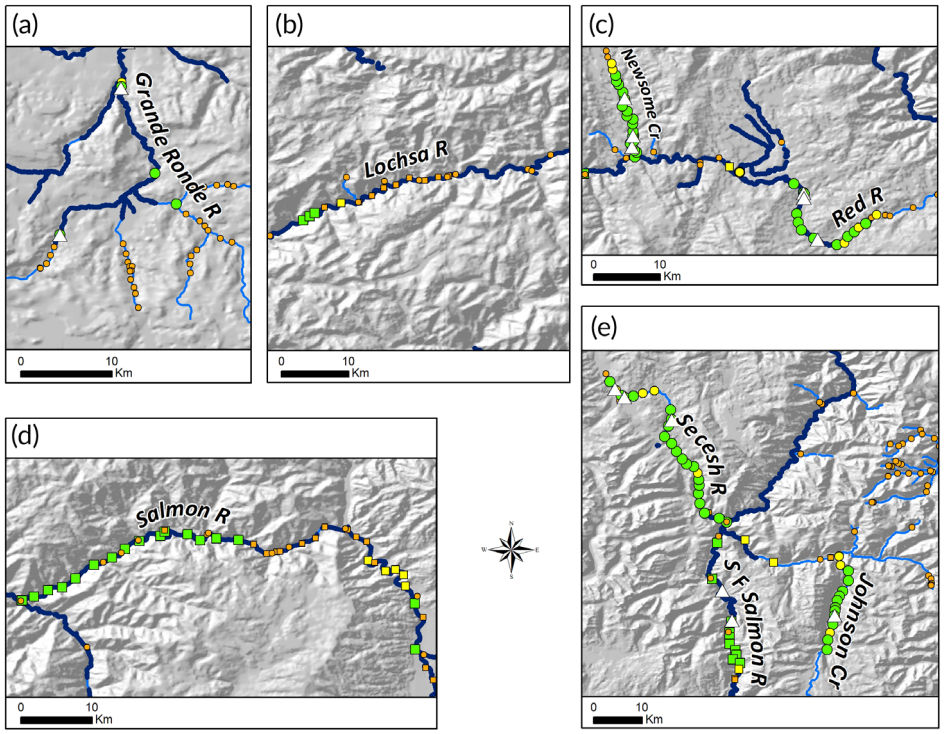

FIGURE 2 Environmental DNA sampling locations (squares, main-stem sites; circles, tributary sites) and translocation sites (white triangles) in five headwater sites (a, Grande Ronde River; b, Lochsa River; c, South Fork Clearwater River; d, Salmon River; e, South Fork Salmon River) in the upper Snake River basin, Idaho-Oregon-Washington. Other details as in Figure 1

spawning locations were potentially occupied by larval lamprey year-round, whereas main-stem habitats may have been seasonally occupied by outmigrating juveniles and returning adults (Jolley *et al.*, 2012; McIlraith *et al.*, 2015; Ostberg *et al.*, 2018). We attempted to identify these potentially occupied habitats for Pacific lamprey in three ways. First, we developed a species distribution model for this portion of the historical range of Pacific lamprey. Pacific lamprey survey data, consisting of site presences and absences from the study area, were downloaded from the U.S. Geological Survey's ScienceBase catalogue (https://www.sciencebase.gov/catalog/item/5745f81fe4b07e28b662c6ee) or digitized from Appendix B of IDFG (2011). This combined data set included 646 survey records but contained many duplicates that were eliminated. Eighty-six sites had also been sampled in multiple years and generally showed consistent

patterns of occupancy, *i.e.*, Pacific lamprey always present or absent. Occupancy status at nine sites, however, changed during the course of sampling, in which case the results of the most recent surveys were assigned to these sites. The final dataset used to develop the species distribution model consisted of 345 unique sites, which were linked to the stream network and reach attribute values described below (Supporting Information Figure S1 and Table S1).

The network within the study area was delineated using the 1:100,000-scale National Hydrography Dataset-Plus Version 2 (NHD-Plus; https://nhdplus.com/NHDPlus/NHDPlusV2_home.php; Moore *et al.*, 2019) and encompassed 56,168 km of streams and rivers. Because channel slope, stream size and temperature are often related to habitat use by Pacific lamprey (Dawson *et al.*, 2015; Reid & Goodman, 2016; Torgersen & Close, 2004), we attributed 1 km reaches (and the sites with observations on lamprey occupancy) with mean annual flow values from the Western U.S. Stream Flow Metrics website (https://www.fs.fed.us/rm/boise/AWAE/projects/modeled_stream_flow_metrics.shtml; Wenger *et al.*, 2010), mean August water temperature values from the NorWeST website (https://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html; Isaak *et al.*, 2017), and slope values developed for NHD-Plus (Moore *et al.*, 2019).

Logistic regression was used to model the probability of Pacific lamprey occurrence as a function of the three habitat attributes using Proc Logistic in SAS Version 9.4. We did not consider a more complex occupancy model to accommodate imperfect detection (*i.e.*, Mackenzie *et al.*, 2006) because detection efficiency estimates for lamprey with conventional sampling techniques are sufficiently high (>0.80; Dunham *et al.*, 2013) and site occupancy, for sites sampled more than once, changed so infrequently that false absences were unlikely to substantially affect covariate parameters (Tyre *et al.*, 2003). Logistic regressions were fit to different candidate models beginning with simple models featuring one of the three reach attributes and progressing in complexity to models with all attributes, two-way interactions and a quadratic effect for stream temperature (to account for nonlinear relations). The models were ranked based on Akaike's information criterion (AIC; Akaike, 1974) and their ability to discriminate among habitats of varying quality was described using the area under the curve (AUC) of the receiver-operating characteristic (Pearce & Ferrier, 2000). Correlations among the three reach attributes were below levels that would cause issues with multicollinearity ($r_{\text{flow}\times\text{temperature}} = 0.50$, $r_{\text{flow}\times\text{slope}} = -0.24$, $r_{\text{temperature}\times\text{slope}} = -0.36$; Dormann *et al.*, 2013). We used the best-fitting model to predict the probability of Pacific lamprey occurrence throughout the study area network; we deemed reaches with probabilities >0.10 as potential habitat.

We recognized that the generality and accuracy of the species distribution model could have been compromised by recent reintroductions and historical declines of Pacific lamprey. Because most site surveys (89%) were conducted prior to 2007 when translocations began (Ward *et al.*, 2012), however, the effect of recent introductions on model performance was expected to be minor. In contrast, by the early 21st century, Pacific lamprey in the Snake River basin had undergone substantial range contractions that were likely driven by passage issues at downstream dams rather than declines in upstream habitat suitability (Clemens *et al.*, 2017). Because others (Gunckel *et al.*, 2009; Wallace & Zaroban, 2013) have observed that habitat for Pacific lamprey often overlaps with that of anadromous salmonids, we broadened our potential habitat template to include streams regarded as currently or historically occupied by Chinook salmon *Oncorhynchus tshawytscha* (Walbaum, 1792), the description of which was downloaded as geospatial files from the StreamNet website (https://www.streamnet.org/). The suitable habitats identified by the species distribution model or that were part of the Chinook salmon network also included all streams into which Pacific lamprey had been recently introduced.

2.4 | Environmental DNA sampling

We designed a comprehensive, systematic, multistage sampling campaign that accounted for the ecology of this species and the high detection probabilities we were likely to realize (cf. Carraro *et al.*, 2021). Previous sampling indicated that detection of Pacific lamprey in turbulent main-stem rivers tended to be longitudinally consistent, *i.e.*, nearly all sites downstream of their presumed headwater extent provided unequivocal positive detections of the target species, and sampling from either river bank yielded similar results (Ann Grote, U.S. Fish and Wildlife Service, unpublished data available *via* the eDNAtlas (Young *et al.*, 2018; for similar results with other species, see Shogren *et al.*, 2019 and Thalinger *et al.*, 2021). Moreover, the limit of detection of the assay we used was 1–2 copies/reaction (Carim *et al.*, 2017) and was coupled with large individual field samples (effective size, 2.5 L). Therefore, we reasoned that a wide sampling interval and samples collected from one side of a river would be sufficient for identifying the overall distribution of Pacific lamprey in major river basins, and collected a single eDNA sample at approximately 20-km intervals in larger channels, *i.e.*, predominantly those with a mean annual flow >20 m^3 s^{-1}, *i.e.*, the Snake, Grande Ronde, Imnaha, Lochsa, Selway and forks of the Clearwater and Salmon Rivers. We also collected a sample from each main-stem tributary (generally 50–100 m upstream from its mouth) that was either deemed potential habitat by the species distribution model or regarded as suitable spawning habitat for Chinook salmon (Supporting Information Figure S2). We regarded a single sample as sufficient because lamprey densities in tributaries were expected to be highest near their mouths and because of the high detection rates for eDNA sampling in such locations (Ostberg *et al.*, 2019). For similar reasons, we concluded that single samples taken across a broader area would be preferable to collecting the many duplicate samples at multiple sites needed for occupancy modelling (Buxton *et al.*, 2021). Samples accessible by road or trail were sampled mostly by federal agency biologists. We collaborated with other agency biologists or citizen scientists that possessed backcountry float permits and boats to obtain samples from otherwise inaccessible reaches, *e.g.*, the main-stem and Middle Fork Salmon River in the Frank Church-River of No Return Wilderness Area, the Selway River in the Bitterroot-Selway Wilderness Area and the Snake

River in Hell's Canyon National Recreation Area. We were unable to obtain samples from the roadless portions of two basins – the lower South Fork Salmon River and middle Grande Ronde River – but sampled extensively in other parts of these basins. Finally, because only publicly accessible sites were sampled, not all potentially or known occupied habitat was sampled in all basins.

A second stage of sampling, at 1–2 km intervals up to and 1–2 km beyond modelled lamprey habitat or the upstream extent of reintroductions, was usually undertaken if a tributary sample was positive for Pacific lamprey DNA and there was ready access to the stream. We also used a 2-km interval to identify the upstream extent of Pacific lamprey in main-stem rivers, beginning at the most upstream point with a positive detection during first-stage sampling and ending at the next point 20 km upstream. Remote or inaccessible sites, *e.g.*, the wilderness portions of the Selway and Middle Fork Salmon Rivers and reaches in the Grande Ronde River basin flowing through private land, were not resampled.

We supplemented newly collected samples with samples archived at the National Genomics Center for Wildlife and Fish Conservation (NGC) in Missoula, MT (portrayed on the eDNAtlas) that were collected within the upper Snake River basin and met our criteria for potential habitat. We also included samples from locations that were not predicted to be occupied by Pacific lamprey, *i.e.*, were not part of the species distribution model or the Chinook salmon networks, but which had previously been analysed for that species, as a test of model accuracy. All new and archived eDNA samples were labelled with a unique site identifier derived from the eDNAtlas and were attributed with estimates of flow, temperature and slope similar to the historical dataset. Because each site in the eDNAtlas represents a roughly 1-km stream reach, samples from slightly different locations could share a site identifier.

All eDNA sampling followed the protocol developed by Carim *et al.* (2016). Briefly, a sample was collected by pumping 5 L of water through a 1.5 μm glass microfiber filter using a peristaltic pump (GeoTech Environmental Services, Denver, CO, USA). If the stream was turbid and the filter clogged before passing 5 L, additional filters were used until 5 L had been sampled. Filters were preserved in silica desiccant and stored individually in plastic bags. The samples were held at ambient temperature in the field and transferred to a freezer (−20°C) at the NGC for analysis. Sample DNA extractions were performed on half of each filter using the Qiagen (Venlo, The Netherlands) DNEasy Blood and Tissue Kit according to the protocol outlined by Franklin *et al.* (2019). The other half of each filter was returned to storage at −20°C. If more than one filter was required to obtain a sample from 5 L of stream water, DNA from half of each filter was extracted.

The samples were analysed in triplicate using quantitative PCR (qPCR) on a StepOnePlus or QuantStudio 3 qPCR instrument (Thermo Fisher Scientific, Waltham, MA, USA) according to methods outlined in Carim *et al.* (2017). A sample was considered positive for Pacific lamprey DNA if amplification exceeded the machine threshold value for fluorescence in at least one of the three qPCR replicates. All reactions included an internal positive control to ensure that the reaction was sensitive to the presence of Pacific lamprey DNA. To avoid spurious positive detections, we re-ran samples producing single-well amplifications that were adjacent to the internal positive control; all such samples remained positive in later runs. Sixteen samples exhibited inhibition, *i.e.*, the mean cycle threshold for the internal positive control for a given sample was delayed >1 cycle compared to the no-template control. If such a sample was positive for Pacific lamprey, no further action was taken; otherwise, we treated the sample with an inhibitor removal kit (Zymo Research, Irvine, CA, U.S.A.) and reanalysed the sample in triplicate. Because the removal of inhibitors by using this method can result in DNA loss, we extracted the second half of the sample filter and combined all of the extracted DNA from a given sample to obtain ∼200 μl of extracted DNA. If a sample was still inhibited after treatment and negative for Pacific lamprey, we analysed the same total volume of DNA across four to six PCR replicates because diluting the amount of DNA in a reaction reduces the effects of inhibitors (McKee *et al.*, 2015). We increased the number of replicates after dilution to keep the potential amount of DNA consistent.

2.5 | Recent observations from conventional data

We used the observations of Pacific lamprey from a state-wide assessment in Idaho (IDFG, 2011) as a baseline for gauging changes in the distribution of indigenous populations. We confined this analysis to basins in Idaho because there were no comparable historical data from streams in north-eastern Oregon and south-eastern Washington. In addition, we treated streams in which Pacific lamprey had been translocated as tests of the efficacy of eDNA sampling for determining the presence of that species. Because eDNA sampling detected Pacific lamprey in every tributary into which they had been stocked (except two, see below) and upstream from each stocking location, we regarded stocking attempts as likely to establish Pacific lamprey and that, in lieu of additional upstream eDNA sampling, a stocking location (Supporting Information Table S3) was a conservative estimate for the upstreammost position of Pacific lamprey in a watershed. We considered the overall distribution of Pacific lamprey in our study area to include all waters downstream from the headwatermost detections or stocking locations – whichever was higher – across all basins to the junction of the Snake and Clearwater Rivers. For this estimate, we reported but ignored nonpositive eDNA detections downstream from occupied headwaters because upstream-migrating adults or downstream-drifting juveniles would inevitably occupy all these waters, even if only temporarily.

3 | RESULTS AND DISCUSSION

Temperature, slope and flow were strong predictors of habitat occupancy by Pacific lamprey. The top model in the candidate set had an AUC of 0.891 and correctly predicted occupancy status at 82.3% of the 345 conventionally surveyed sites at a classification threshold (0.64) that balanced errors of commission and omission (Tables 1 and 2). Occupancy peaked between 18 and 19°C, and declined at cooler

TABLE 1 Rankings for logistic regression models that predicted occurrence probabilities of Pacific lamprey at 345 historical survey sites

Model	Covariates[a]	ΔAIC	AUC
1	T, T^2, F, S, T × F	0	0.891
2	T, T^2, F, S, T × F, T × S	0.2	0.892
3	T, T^2, F, S, T × F, T × S, S × F	1.4	0.894
4	T, T^2, F, S	26.1	0.868
5	T, T^2, F, S, S × F	26.1	0.869
6	T, T^2, F, S, T × S	28.1	0.868
7	T, T^2	45.9	0.853
8	T, F, S	58.1	0.836
9	T	97.1	0.806
10	S	109	0.742
11	F	169	0.809

[a]*Note*. F, mean annual flow; S, reach slope; T, mean August stream temperature.
Models are ranked from most plausible (ΔAIC = 0) to least plausible, and the area-under-the-curve (AUC) of the receiver-operating characteristic provides a measure of model performance across a range of sensitivities and specificities. Model 1 was selected to predict probabilities of occurrence and delimit the potential distribution of Pacific lamprey for subsequent eDNA sampling.

TABLE 2 Parameter estimates of the logistic regression model that was developed using historical surveys and used to predict Pacific lamprey occurrence probabilities that guided subsequent eDNA sampling

Covariate	*b*	SE	*P*
Intercept	−45.5	8.9	<0.01
Temperature	4.98	1.03	<0.01
$Temperature^2$	−0.133	0.030	<0.01
Slope	−0.693	0.271	0.01
Flow	0.0488	0.0128	<0.01
Temp×flow	−0.0023	0.0006	<0.01

and warmer temperatures, peaked at slopes <1% and decreased at higher values, and increased with stream size except in the warmest streams because of an interaction between temperature and flow (Figure 3). Predictions from this model indicated that 4284 km, or 8% of the initial NHD-Plus network description, constituted potential habitat. Addition of Chinook salmon streams beyond that extent added 6331 km to create a potential habitat network of 10,615 km from which we chose locations for eDNA sampling (Supporting Information Figure S1).

Overall, we analysed samples from 671 unique locations assigned to 624 sites identified in the eDNAtlas (with one to four unique locations sampled at each eDNAtlas site) for the presence of Pacific lamprey DNA (Supporting Information Table S2). These sites represented a broader range of environmental conditions than those used to build the species distribution model, in part reflecting the targeting of smaller, colder and steeper streams for reintroductions (Figure 4). In addition, 89 archived samples (representing 87 sites, collected between August 4, 2015 and July 27, 2020) previously analysed for the presence of Pacific lamprey were collected from tributaries that, although part of the basins in which Pacific lamprey are native, were not within the potential habitat network. These samples were regarded as a test of the comprehensiveness of our potential habitat estimate, in that we expected them to be unoccupied. Because Pacific lamprey DNA was not detected at any of these sites, we did not consider them further. Of the remaining 582 samples collected from potential habitat at 537 sites, 394 samples were collected (from June 4, 2018 to July 21, 2021) as part of this project, supplemented by 187 archived samples collected (from August 3, 2015 to September 16, 2020) for other projects (Table 3).

We obtained positive detections of Pacific lamprey in 208 samples (from 199 sites) taken during every month of collection, *i.e.*, June through October. Most detections of Pacific lamprey involved amplification of all three replicates (three replicates, 78.4%; two replicates, 10.5%; one replicate, 11.1%), indicative of moderate to large quantities of eDNA in most samples. Positive samples that did not amplify in all three wells were generally obtained from lower river main stems well downstream of suspected spawning locations, *e.g.*, Middle Fork Clearwater River and lower Salmon River, or near the upstream limit of occupied habitat, *e.g.*, South Fork Salmon River, Secesh River, Newsome Creek and Red River (Figures 1 and 2). We hypothesize that lower main-stem sites are diffusely occupied habitats primarily used during migration or over winter by adults, juveniles or older larvae, in part because these are among the warmest locations in summer (IDFG, 2011; Jolley *et al.*, 2012). In addition, it may reflect the effects of dilution of DNA arising from distant upstream sources (Pont *et al.*, 2018; Thalinger *et al.*, 2021; Wood *et al.*, 2021). The often-weaker headwater signals are suggestive of reduced densities and discontinuous habitat occupancy near the upstream extent of their distribution (cf. Penaluna *et al.*, 2021). Combinations of strong detections, weak detections and nondetections in proximity to eDNA sources are common in caged-fish studies (Jane *et al.*, 2015; Robinson *et al.*, 2019; Thalinger *et al.*, 2021) and would be expected at the upstreammost extent of populations in which mixing of eDNA from target individuals throughout a river cross-section is incomplete (Thalinger *et al.*, 2021; Wood *et al.*, 2020, 2021). These longitudinal trends in lamprey eDNA are consistent with patterns observed in smaller watersheds (Duda *et al.*, 2021; Ostberg *et al.*, 2019).

We estimated that 1875 km of lotic habitat was occupied by Pacific lamprey in the upper Snake River basin. Occupancy in 431 km of streams – the Lochsa, Selway and Imnaha River basins and the Salmon River basin upstream from the mouth of the South Fork and Snake River between the mouths of the Grande Ronde and Imnaha Rivers – was unlikely to be the result of, or influenced by, recent translocations because these locations were never stocked and were tens of kilometres distant from tributary stocking locations in other basins. Pacific lamprey DNA was recovered from most locations in river main stems downstream from where Pacific lamprey had been observed prior to reintroductions (IDFG, 2011). In these river headwaters, however, the headwatermost detections of Pacific

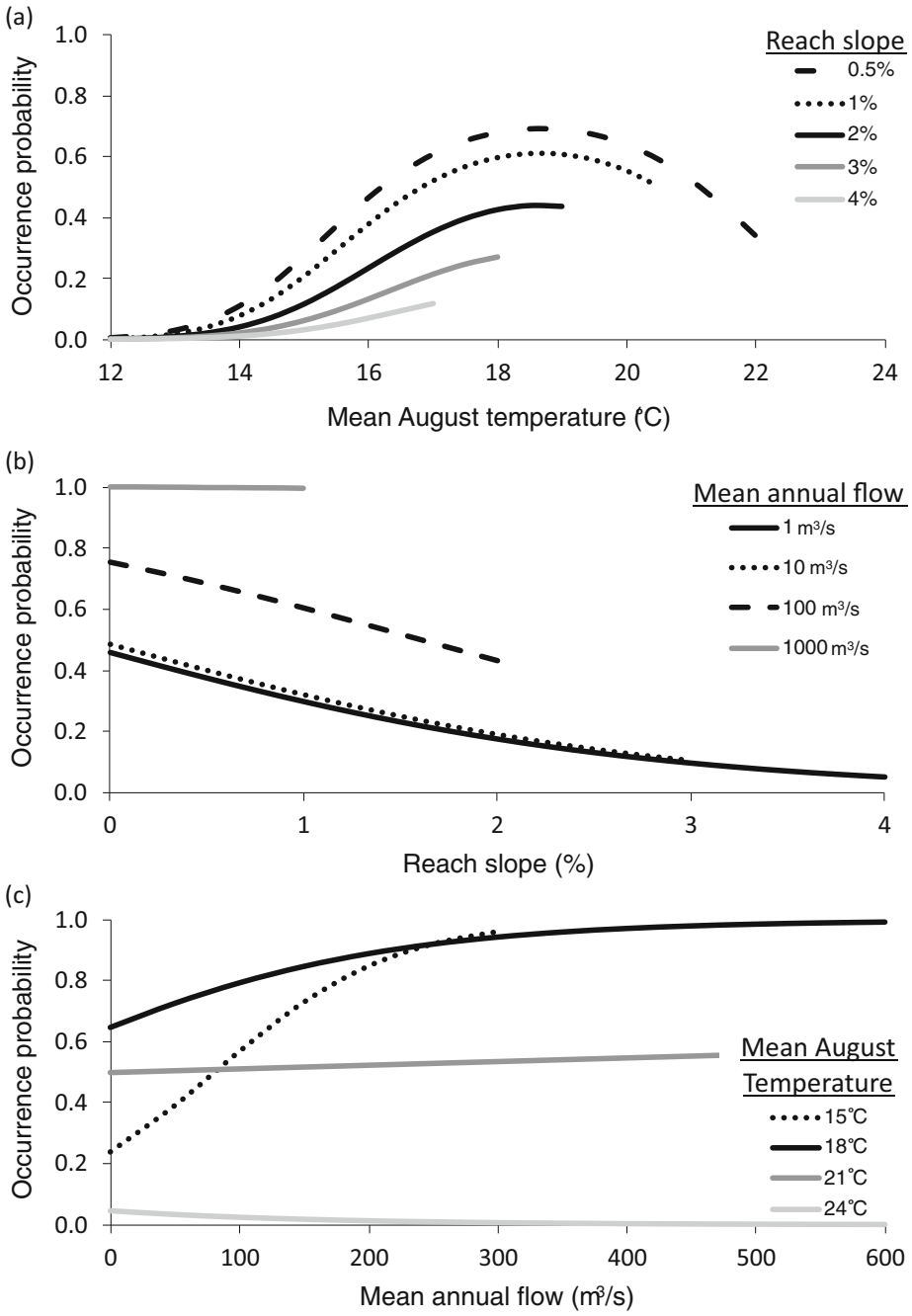

FIGURE 3 Response curves from a logistic regression model that was developed using historical surveys and used to predict Pacific lamprey occurrence probabilities that guided subsequent eDNA sampling. Curves are conditioned on the median value of the third covariate not depicted in a panel and are truncated to avoid extrapolation beyond conditions that occurred within the study area stream network

lamprey were either downstream from those a decade earlier (range 10.1–65.2 km) in the Lochsa, Snake and Middle Fork Salmon Rivers, relatively unchanged in the Selway River (downstream 3.0 km) or farther upstream in the Salmon River (27.4 km; IDFG, 2011). More ambiguous was the limited area of occupancy in the Imnaha River (Supporting Information Table S2; McIlraith *et al*., 2015). Although the isolated, single detection in this basin was spatially consistent with historical and recent observations (https://nrimp.dfw.state.or.us/FHD_FPB_Viewer/index.html), this distributional pattern was unusual and at best indicative of a very small population. We did not observe unassisted recolonization of any larger, formerly occupied basins, *e.g*., the Potlatch River or Snake River below Hells Canyon Dam.

There was no evidence that indigenous populations of Pacific lamprey remained in any tributary habitats in the upper Snake River basin. Traditional ecological knowledge and museum collections note their presence in several tributary streams in the upper Snake River basin, *e.g*., Lolo and Newsome Creeks, but not since the early 2000s (IDFG, 2011). The modelled probabilities of occupancy were relatively high (>0.40) in many larger tributaries (Supporting Information Figure S2), and similar habitats are commonly used elsewhere within the historical range of this species (Dunham *et al*., 2013; Gunckel *et al*., 2009; Torgersen & Close, 2004). The failure of this species to occupy apparently suitable habitat higher in main-stem rivers in Idaho is also puzzling. This absence, coupled with widespread successful recruitment following translocations in tributaries, suggests that

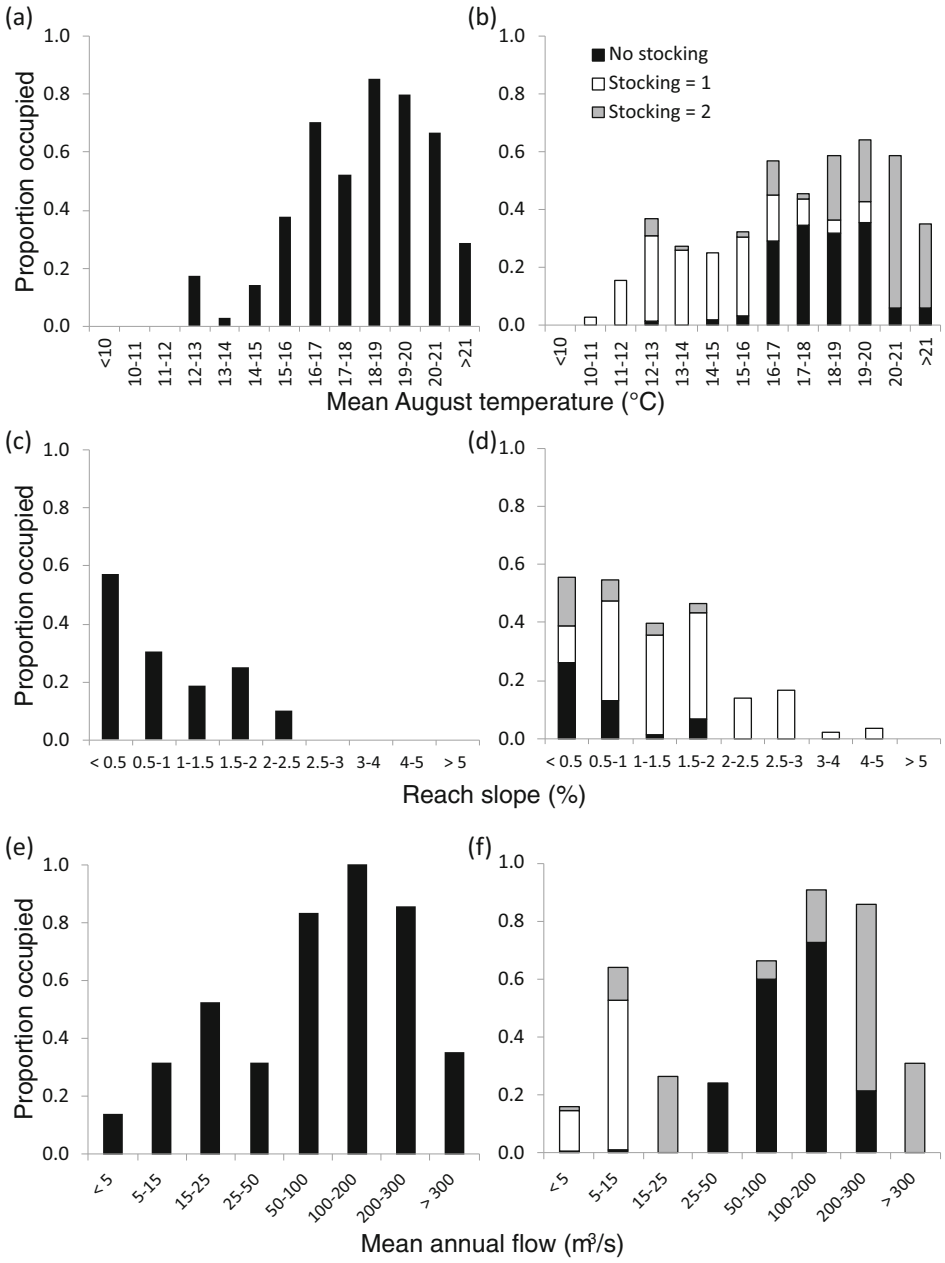

FIGURE 4 Pacific lamprey habitat occupancy, based conventional sampling (panels a, c, and e) and eDNA sampling (panels b, d, and f), relative to mean August water temperature, reach slope and mean annual flow. The eDNA samples are categorized for portions of the network not influenced by stocking (black bars), directly influenced by stocking (white bars) or downstream from stocked areas (grey bars)

access to and availability of suitable upriver and tributary spawning habitat is not limiting Pacific lamprey populations in this region (Clemens *et al*., 2017). Insufficient time has passed, however, to test this hypothesis using returns of offspring from translocated adults because the generation time for Pacific lamprey in this basin may exceed 15 years (Hess *et al*., 2022).

In contrast, positive detections of Pacific lamprey were the norm in nearly all basins receiving adult translocations, and often at locations distant from the translocation sites. In 19 tributaries or main-stem headwaters that had been seeded with reproductively mature adults, we detected Pacific lamprey at nearly all sites downstream from these introductions, generally to the mouths of each stream. In many of these areas, *i.e*., the South Fork Salmon River basin, Asotin Creek and most tributaries to the Middle Fork and South Fork Clearwater River, headwater stocking of adults and subsequent production and downstream drift of larvae likely explain the extensive downstream detections in many tributary and main-stem habitats because Pacific lamprey were believed to be extirpated from these waters, whereas remnant indigenous populations may be contributing to the pattern in other areas, *e.g*., the upper South Fork Clearwater River and much of the Grande Ronde River basin. Overall, it appeared that stocking efforts were nearly always successful, and that eDNA sampling corroborated conventional data on population establishment (Ward *et al*., 2012). In two instances, however, we failed to detect Pacific lamprey DNA in stocked streams in the Grande Ronde River basin, but both involved samples from single sites for which there were mitigating circumstances. In Little Lookinglass Creek, conventional surveys have also failed to detect Pacific lamprey; this stream is

TABLE 3 Descriptive statistics for stream conditions at conventional and eDNA survey sites that were used to describe the distribution of Pacific lamprey in the study area

Data set	Covariate	Lamprey occurrence	*n*	Mean	Median	SD	Minimum	Maximum
Conventional	Temperature (°C)	0	219	14.6	14.3	2.96	8.34	22.1
		1	126	17.3	16.8	2.04	12.1	22.3
	Slope (%)	0		1.25	0.84	1.33	0.01	8.02
		1		0.51	0.39	0.67	0.01	2.12
	Flow ($m^3\ s^{-1}$)	0		67.6	2.70	249	0.09	1172
		1		94.5	58.2	160	0.07	1168
eDNA	Temperature (°C)	0	425	13.9	14.0	3.18	6.7	22.2
		1	199	16.0	16.2	2.58	11.0	22.1
	Slope (%)	0		3.87	2.57	3.83	0.01	20.1
		1		0.73	0.57	0.71	0.01	4.49
	Flow ($m^3\ s^{-1}$)	0		28.8	0.75	140	0.01	1169
		1		55.1	8.19	112	0.17	1172

Note. Measurement units are in parentheses.

steep and may have little spawning habitat, thus adults may have dispersed shortly after stocking (Aaron Jackson, Confederated Tribes of the Umatilla Indian Reservation, personal communication). Similarly, this reach was colder (11.63°C; Supporting Information Table S2) than all but four occupied reaches in the study area, and adults may have sought warmer locations or spawning efforts were unsuccessful (Dawson *et al*., 2015). In Five Points Creek, stocking led to recruitment of larval Pacific lamprey and an upstream eDNA sample (analysed by another laboratory) was positive for this species (Paul Sankovich, U.S. Fish and Wildlife Service, unpublished data), whereas the eDNA sample we analysed from near the mouth did not indicate species presence. This sample, however, was collected downstream from a dewatered section, and it is likely that subterranean flow dramatically increased flow time-of-travel and increased DNA removal *via* deposition or adsorption (Fremier *et al*., 2019; Ogram *et al*., 1988; Pont *et al*., 2018).

The eDNA sampling also identified upstream redistribution from introduction sites. In stocked streams with fine-scale sampling, eDNA-based detections were often substantially upstream from the introduction sites ($n = 6$ streams with estimates, range 1.8–36.0 km), consistent with patterns of movement among radio-tagged adults following their release in tributary streams (Ward *et al*., 2012). These observations imply that reintroduced adults explore widely for suitable spawning locations within a particular tributary. Hence, stocking in one or two locations within many tributaries with suitable habitat may be more strategic for re-establishing Pacific lamprey throughout a river basin rather than concentrating most or all introductions at different points in a single stream.

We acknowledge that eDNA sampling has weaknesses that are widely recognized, including for sampling Pacific lamprey (Clemens *et al*., 2022). Environmental DNA transport in larger river systems tends to promote detections well downstream of individuals releasing DNA (Pont *et al*., 2018; Robinson *et al*., 2019), so the downstream terminus of habitat occupancy, if present, is uncertain. We were also uncertain about which life stage may have produced the positive detections. Although all such locations plausibly supported larval forms, some of the detections may also have resulted from recently translocated, naturally returning or overwintering adults, decaying carcasses following spawning or downstream-migrating juveniles (Dawson *et al*., 2015; Hess *et al*., 2022), although this was immaterial for the delineation of occupied habitat. Finally, eDNA-based detection of Pacific lamprey, while regarded as very high, may still fail to detect this species when it is present and warrant repeat sampling at a site (Burian *et al*., 2021). Along these lines, five of our sampling sites provided conflicting results in which lamprey were not detected on all sampling occasions. Although this could result from variation in detectability, it is notable that the samples at each site were collected across 1–2 years, and in each instance the more recent samples produced positive detections whereas the older samples did not. Most of these involved streams selected for adult translocations. Given the strong and longitudinally consistent detections of Pacific lamprey across most of the sampling network, that samples from 33 other sites visited more than once produced the same results on all sampling occasions and the extremely high detection probabilities generally obtained from eDNA sampling for this species (Carim *et al*., 2017; Ostberg *et al*., 2019), perhaps the most parsimonious explanation for sites with conflicting data is that the later samples were detecting recently introduced adults or larvae produced by previous introductions, thus reflecting genuine differences in occupancy rather than imperfect detection. Likewise, we regard the aforementioned failure to resolve the distribution of Pacific lamprey in the two stocked streams, Little Lookingglass and Five Points Creeks, a consequence of inadequate spatial coverage, not the failure of eDNA sampling *per se*.

4 | CONCLUSIONS

Overall, this work establishes a benchmark for the distribution of Pacific lamprey in the upper Snake River basin that can form the basis

for future assessments of its status. The species undoubtedly occupies a fraction of its historical range in the basin, but the precise extent of its former range in accessible habitats is uncertain because of a lack of historical collections (IDFG, 2011). Nevertheless, over the last decade there appear to have been further contractions in the upper portions of some river main stems, whereas the presence of Pacific lamprey in tributaries and some main-stem rivers has expanded as a consequence of the translocation and spawning of mature adults. Although this study has addressed one of the primary shortcomings in our understanding of Pacific lamprey – the extent of their distribution in individual drainages (Reid & Goodman, 2015) – for a substantial portion of the upper Snake River basin further work is warranted because sampling was incomplete or imprecise in areas with poor access, ongoing recovery actions continue to alter this distribution and climate-related issues may lead to further declines among indigenous populations (Isaak, Luce, *et al*., 2018; Wang *et al*., 2020). A critical adjunct, however, is to extend this work across the remainder of the range of Pacific lamprey to provide a comprehensive view of the status of this species.

Although eDNA sampling for species presence is a relatively young field (Ficetola *et al*., 2008) which has yet to settle on a standardized approach (Cristescu & Hebert, 2018), its many advantages over conventional methods and a better understanding of its error structure (Burian *et al*., 2021) have led to its increasing acceptance for regional or national assessments of species distributions (Kasai *et al*., 2021; King *et al*., 2022; Matter *et al*., 2018). We believe that many elements of this study can serve as a template for using model-driven eDNA sampling as the basis for the high-resolution, broad-scale assessments of species of conservation concern. The species distribution model was built from broadly available geospatial stream predictors and online sources of conventionally collected data, to which the recently collected eDNA data can be added to enhance future such models (cf. Riaz *et al*., 2020). The spatial domain was systematically sampled to ensure even coverage of all potential habitat and to maximize our scope of inference (Clemens *et al*., 2022). The majority of samples were collected in a relatively brief period by a small group of biologists and citizen scientists, yet resolved the distribution of a single species across over 10,615 km of potential habitat (itself derived from a 56,168 km stream network). This work also reaffirmed the value of previously collected eDNA samples as a biodiversity archive (Jarman *et al*., 2018), to which the samples collected as part of this study can now contribute. Finally, to leverage the rapid growth in the application of eDNA sampling to a host of taxa across the globe, we encourage the continued development of publicly accessible sample repositories and sampling results (Berry *et al*., 2021) and the increasing participation of nonspecialists (*e.g*., as in the California Environmental DNA project; https://ucedna.com/) to facilitate similar broad-scale – and eventually long-term – studies of aquatic biodiversity.

AUTHOR CONTRIBUTIONS

M.K.Y., D.J.I., D.N., K.J.C. and B.R. conceived the design. M.K.Y., D.J.I., D.L.H., K.J.C. and T.W.F. contributed to the field sampling. V.A.Z. conducted the majority of the sample analyses. M.K.S. provided project oversight. M.K.Y. wrote the initial draft, D.L.H. prepared the figures and all authors contributed to the final version.

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SIGNIFICANCE STATEMENT

The sampling of environmental DNA (eDNA) promises to revolutionize broad-scale and range-wide species assessments, especially if applied systematically, widely and efficiently, *i.e*., only in locations that could represent habitat for the species of interest. As an example, we crafted a model-driven spatial sampling template and executed an eDNA-based sampling campaign led by professionals and volunteers, supplemented with previously collected samples, to determine that Pacific lamprey *Entosphenus tridentatus* occupied 1875 km of the 56,168 km upper Snake River basin in the north-western United States, and that its presence in over 1400 km was likely to be influenced by restoration stocking of that species. This approach could serve as a guide for range estimates of other wide-ranging aquatic species of conservation concern.

ORCID

Michael K. Young https://orcid.org/0000-0002-0191-6112

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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