Lifetime Trophic Ecology of Fishes and Invasive Species Management in Dryland Streams

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Abstract

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Invasive species are one of the greatest threats to freshwater fish biodiversity, with numerous documented impacts on freshwater food webs. This threat is especially acute in the American southwest, a region that is home to many endemic freshwater fishes. Invasive fish impacts have been studied most often at discrete points in time for pairs of species, but knowledge gaps remain regarding impacts across ontogeny in multi-species communities. Stable isotope analysis is commonly used to infer trophic ecology, including species interactions through competition and predation. We used a novel method of fish eye lens stable isotope analysis coupled with otolith growth measurements to construct lifetime trophic trajectories for native and nonnative fishes in Burro Creek, Arizona. Our results provide support for asymmetric competition wherein native species exhibited displaced trophic trajectories with respect to $\delta^{13}C$ and $\delta^{15}N$, which may lead to reduced fish growth and fitness, with implications for population persistence.

Competition for shared resources is a powerful mechanism in community ecology, contributing to the success of many invasive species. The balance between intra- and inter-specific competition is predicted to influence species coexistence, with theoretical and empirical studies historically focusing on single life stages. However, many fish species undergo ontogenetic dietary shifts, resulting in dynamic competitive interactions. Using the lifetime trophic trajectories of fishes from Burro Creek, Arizona, we measured isotopic niche distance as a proxy for competitive interaction strength and found shifts in competition through ontogeny within and between native and nonnative species pairs.

Invasive species are increasingly targeted for suppression or eradication to reduce impacts on native communities. We leveraged two invasive green sunfish removal programs in intermittent streams of the Bill Williams River, Arizona, to quantify removal success and explore alternative effort allocation in time and space. Bayesian hierarchical modeling of removal data was used to estimate demographic parameters, finding that both removal programs resulted in at least a 0.39 probability of eradication. Simulated alternative management scenarios revealed that population suppression could be achieved with reduced effort, but eradication success was dependent on the high frequency of removal events, even after zero fish were captured. Given the accelerating spread of invasive species and limited resources to control invasive populations, quantitative removal models are valuable tools for improving and evaluating invasive species removal efforts.

Though native to the Columbia River Basin, northern pikeminnow have been the subject of long-term population control. This began in response to their increased predation of anadromous juvenile salmonids as a result of habitat modification due to hydropower dam construction. The Northern Pikeminnow Management Program (NPMP) is a targeted harvest program with a sport reward fishery that has been operating in the Columbia and Lower Snake Rivers since 1991. Northern pikeminnow are tagged annually to model their exploitation rate, and the model used assumes closed populations separated by dams. We studied the movement of northern pikeminnow using passively collected passive integrated transponder (PIT) tag data from 2003-2022. Movement records reveal that individuals traveled at least as far as 968 km. Nearly 13% of northern pikeminnow tagged through the NPMP were detected in different river sections, separated by dams, from where they were initially tagged. Our increased understanding of northern pikeminnow movement informs the calculation of the exploitation rate, one of the key measures of NPMP success, and may contribute to future management strategies.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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DEDICATION

For my son, Mouctar, I hope you always follow your dreams.

Chapter 1. INVASIVE SPECIES INVOKE A LIFETIME OF TROPHIC CHANGE IN NATIVE STREAM FISHES

Publication history: This study was co-authored with Julian D. Olden and has been published in *Ecosphere* (citation below).

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1.1 ABSTRACT

Trophic interactions operate across the lifetime of an individual organism, yet our understanding of these processes is largely limited to a single life-stage or moment in time. Management and conservation implications of this knowledge gap are particularly important given the mounting number, spread, and ecological impacts of invasive species. Biotracers such as carbon and nitrogen stable isotopes of animal muscle, for example, are commonly used to characterize the trophic ecology of an individual, but fail to capture intra-individual variation and ontogenetic dietary shifts. However, recent work suggests that eye lenses may facilitate the reconstruction of individual lifetime trophic trajectories for fishes, including the chronology of past trophic positions of and carbon flow to consumers. By combining stable isotope analysis of fish eye lens tissue with aging techniques (otolith growth measurements), this study is the first to ask how the lifetime trophic niches of individuals vary within different community contexts. The results provide evidence for asymmetric competition causing differing trajectories in lifetime trophic niches for native and nonnative fishes along an invasion gradient in Burro Creek, Arizona, USA. Native roundtail chub, Sonora sucker, and desert sucker all displayed a coordinated displacement of lifetime trophic trajectories to a lower trophic level and reliance on aquatic, rather than terrestrial, resources as indicated by a shift to lower $\delta^{13}C$ and $\delta^{15}N$ in mixed, relative to native-only, communities. By contrast, the trophic trajectories of nonnative green sunfish and bullhead species remained consistent between native- and nonnative-dominated communities. The presence of nonnative species led to a significantly greater decrease in $\delta^{13}C$ through ontogeny for roundtail chub, a species of conservation concern in Arizona. These results demonstrate the prolonged trophic impact of nonnative fishes on native fishes beyond a single life stage. Displacement of ontogenetic dietary shifts by native fishes through interactions with nonnative species may lead to reduced fish growth and fitness, with implications at the population and ecosystem levels. Fish eye lens stable isotope analysis offers new opportunities to study the lifetime chronology of individual feeding habits, and allows for exploration of the impacts of invasive species and environmental change throughout ontogeny.

1.2 INTRODUCTION

Aquatic invasive species are a significant contributor to freshwater species imperilment across the world (Reid et al. 2019), compromising biological structure and function through an array of biotic interactions (Gallardo et al. 2016). Direct effects of top-down predation can lead to reduced population sizes of native species (Eby et al. 2006; Mollot, Pantel, and Romanuk 2017). Even the presence of an invasive predator can affect prey foraging behavior, resulting in non-consumptive effects (Lima 1998; Kindinger and Albins 2017). Indirect impacts on native species may occur through competition between freshwater invasive and native species (Jackson et al. 2017). In total, invasive species have numerous direct and indirect effects on recipient food webs by creating novel trophic links and modifying or disrupting existing ones involving native species (David et al. 2017).

Competition is a particularly important mechanism of aquatic invasive species impacts (Chen et al. 2023; Gallardo et al. 2016). An invader may compete with the native species for limited resources (exploitative competition) or exhibit antagonistic actions during feeding (interference competition; Schoener 1983). For example, food webs have been substantially restructured by invasive smallmouth bass (*Micropterus dolomieu*) in some North American lakes, competing with native lake trout (*Salvelinus namaycush*) and shifting them to a lower trophic position (Vander Zanden, Casselman, and Rasmussen 1999; Lepak, Kraft, and Weidel 2006). Similarly, competition with invasive round goby (*Neogobius melanostomus*) led native white sucker (*Catostomus commersonii*) to shift their feeding habits in tributaries of the Laurentian Great Lakes (Kindree, Jones, and Mandrak 2023). In many cases, invasive species are superior competitors with an advantage over native species (Bøhn and Amundsen 2001; Bergstrom and

Mensinger 2009; Dominguez Almela, South, and Britton 2021), although the direction and magnitude of competition depend upon the specific identities of the native and nonnative species.

The study of invasive species impacts has advanced considerably with the use of biotracers such as stable isotopes of carbon and nitrogen to examine trophic ecology and identify traits that contribute to or limit invasion success (Bodey, Bearhop, and McDonald 2011; Cucherousset et al. 2012; McCue et al. 2020). In contrast to stomach content analysis that provides a single snapshot in time, the time period covered by a measured stable isotope ratio is dependent on the tissue selected and its elemental turnover time (Fry 2006). Effects of invasive fishes on native fish trophic niches (feeding habits) have been quantified using stable isotope analysis (SIA; Walsworth, Budy, and Thiede 2013; Jackson et al. 2016; Dominguez Almela, South, and Britton 2021). The trophic niche of a species can be inferred using its isotopic niche, as measured by carbon and nitrogen stable isotope ratios (Newsome et al. 2007). The strength of competitive impacts can be derived from the degree of overlap between isotopic niches of native and nonnative species, although competition can also result in trophic niche divergence (Tran et al. 2015; Pennock et al. 2021). However, many past studies share two limitations. First, SIA on fin clip or muscle tissue of individuals only integrate feeding habits over a span of several months during a single, and often the most recent, life stage (Jardine et al. 2005; Miller 2006). Second, investigations of temporal changes in trophic niche ecology have been largely limited to SIA of multiple tissues with varying incorporation rates, individuals sampled through multi-year monitoring, or archived museum specimens collected over time.

Life-long isotopic niches of individual fish can be reconstructed using different tissues that record the chronology of feeding habits, including scales (Olden et al. 2019), vertebrae (Estrada et al. 2006), and eye lenses (Wallace, Hollander, and Peebles 2014). While not commonly examined, fish eye lenses have been used in a few instances to track lifetime changes in dietary isotopic values due to their incrementally grown, metabolically inert, proteinaceous tissue (Wallace, Hollander, and Peebles 2014; Tzadik et al. 2017; Quaeck-Davies et al. 2018; Bell-Tilcock et al. 2020). Fish eye lenses are grown in concentric, spherical layers (laminae) which are formed when fiber cells elongate and undergo a form of attenuated apoptosis (Bloemendal et al. 2004; Quaeck-Davies et al. 2018). Eye lens diameter growth is proportional to total body growth with species-specific regression parameters (Quaeck-Davies et al. 2018; Curtis et al. 2020). This increase in length is a step function of lens diameter rather than a continuous increase, resulting in discrete laminae formed approximately every 2-3 months (Wallace, Hollander, and Peebles 2014; Granneman 2018). Eye lens stable isotope values are typically measured as a function of eye lens layer midpoint or estimated fish length, which limits comparisons between populations and species. However, otolith growth measurements may be used to relate eye lens layer stable isotope values to fish age, allowing for a common scale of comparison (Tzadik et al. 2017), although this has yet to be done.

Ontogenetic dietary shifts can be analyzed using these chronological records of trophic ecology information, potentially offering novel insight into how dietary changes over an individual's lifetime may be influenced by both abiotic and biotic factors, including environmental variability and species interactions (Sánchez-Hernández et al. 2017; 2019). Ontogenetic dietary shifts are well-recognized in freshwater fish species that exhibit corresponding changes in habitat, such as Eurasian perch (*Perca fluviatilis*; Collette et al. 1977), Clear Lake hitch (*Lavinia exilicauda*; Young et al. 2022) and bluegill sunfish (*Lepomis macrochirus*; Werner and Gilliam 1984). In addition to habitat use, other drivers of ontogenetic dietary shifts in fishes include competition, predation risk, and prey availability (Sánchez-Hernández et al. 2019). Questions regarding whether invasive species invoke disruptions to ontogenetic dietary shifts of native species remain unanswered. Previous research has focused almost exclusively on the trophic impacts of invasive species on single life stages, despite the expectation that invasive and native species are interacting across their entire lifespans. Predator avoidance may inhibit ontogenetic dietary shifts of juveniles by limiting habitat use associated with higher prey availability (Kimirei et al. 2013), whereas interspecific competition may directly promote ontogenetic dietary shifts to reduce overlap in resource use (Persson and Greenberg 1990; Sánchez-Hernández et al. 2019). Unlike assemblages of native species that have co-evolved together, nonnative species introductions contribute to novel communities with the potential to disrupt well-established food web interactions (Baxter et al. 2004; Wainright et al. 2021).

Riverine ecosystems have a long history of species invasions, resulting in predation and competitive impacts on native species that threaten their persistence and recovery efforts. This ecological threat is especially evident in dryland rivers of the American Southwest (Minckley and Deacon 1968; Olden, Poff, and Bestgen 2006). In these river systems, invasive species have fundamentally changed fish community composition (Pool and Olden 2012), with many notable examples of resulting food web impacts (Dudley and Matter 2000; Rogosch and Olden 2020; Walsworth, Budy, and Thiede 2013). Intensifying interactions with nonnative fishes coupled with the effects of dams and hydroclimatic alterations continue to drive declines in many native fishes of the region (Ruhí, Olden, and Sabo 2016; Kominoski et al. 2018; Gido et al. 2023).

The present study is the first to quantify the potential impacts of invasive species on the lifetime trophic trajectories of native fishes with differing feeding habits by tracking temporal changes in dietary isotopic values from eye lenses combined with otolith growth measurements. Specifically, we examine the effects of species invasions on the trophic ecology of native fishes of western Arizona, United States. These endemic, native species have co-evolved over millennia and occupy distinct trophic niches (Minckley and Marsh 2009). Roundtail chub (*Gila robusta*) are omnivores that become more piscivorous through ontogeny, while Sonora suckers (*Catostomus insignis*) largely consume aquatic invertebrates, and desert suckers (*Catostomus clarkii*) are primarily herbivorous, relying heavily on algae and detritus (Minckley and Marsh 2009). The most common nonnative species, green sunfish and bullhead (*Ameiurus spp.*), are generalist omnivores, both capable of piscivory when they reach larger sizes (Moyle 2002). Our overarching question is: how do the lifetime trophic trajectories of native and nonnative fish species, revealed using SIA of eye lens tissue, vary across an invasion gradient? First, we expect that native species' lifetime trophic trajectories are displaced in mixed native-nonnative assemblage communities relative to native-only communities, with roundtail chub and Sonora sucker exhibiting the greatest trophic displacement because of high dietary overlap with the nonnative species. Furthermore, we expect higher intraspecific variability in trophic displacement for roundtail chub given the greater feeding plasticity offered by omnivory. Second, we posit that nonnative species will display more consistent lifetime trophic trajectories regardless of native species abundance in mixed-assemblage communities, owing to their competitive superiority.

1.3 METHODS

Study system: Burro Creek is a tributary of the Bill Williams River (Arizona, USA), with a watershed area of 1,850 km^2. Vegetation ranges from Sonoran desert scrub and Great Basin conifer woodland in the headwaters, to dense riparian forests, dominated by native cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*) trees on the floodplains. The fish communities of Burro Creek show marked turnover over a very short watercourse distance, with the middle reaches and headwaters containing only native species and lower reaches containing high abundances of nonnative fishes. This invasive gradient has defined Burro Creek for many years because intermittent stream sections preclude or slow the upstream movement of nonnative fishes, some of which were stocked downstream into Alamo Reservoir (Pool and Olden 2015). The native fishes in Burro Creek are common to the lower Colorado River Basin and include desert sucker, Sonora sucker, roundtail chub, speckled dace (*Rhinichthys osculus*), and occasional longfin dace (*Agosia chrysogaster*). Desert sucker, Sonora sucker, and roundtail chub are considered vulnerable species of concern due to habitat loss and impacts from nonnative species. Nonnative fishes include green sunfish, black bullhead (*Ameiurus melas*), yellow bullhead (*Ameiurus natalis*), red shiner (*Cyprinella lutrensis*), and occasional fathead minnow (*Pimephales promelas*) and common carp (*Cyprinus carpio*).

Fish sampling: We surveyed 9 locations across the longitudinal invasion gradient from lower Burro Creek to its headwater tributaries between April 1-12, 2021 (Fig. 1.1). Fish were captured using backpack electrofishing, and occasional opportunistic seining to target larger individuals in deep pools. The length of each sample reach was approximately 20 times channel width. One-pass electrofishing was employed using a Smith Root 24 Backpack Electrofishing Unit with a standard anode (25 cm diameter ring attached to a 2m pole) and cathode (3.2m wire cable) following standard protocols (Bonar, Hubert, and Willis 2009). All captured fish were identified to species and total abundance was enumerated. A subset of fish representing a range of sizes were humanely euthanized and placed directly in a cooler with dry ice for subsequent analyses of stable isotopes and otolith aging. A total of 1,647 fish were captured comprising 11 different species in the Burro Creek watershed. The six most common large-bodied fish species (roundtail chub, Sonora sucker, desert sucker, green sunfish, yellow bullhead, black bullhead) are the focus of this study due to their larger eye lenses allowing the creation of stable isotope time series. Primary producer and benthic macroinvertebrate samples were collected from each site to measure the stable isotope values of basal resources and primary consumers. Periphyton, specifically filamentous algae, and coarse particulate organic matter, specifically decaying leaf litter, represented the primary producers. Benthic macroinvertebrates were captured using a D-frame net and identified to family when possible. A total of 35 distinct taxa were identified and

10 of the most common taxa across sites, representing collector/filterer, collector/gatherer, scraper, and predator functional feeding groups were processed for stable isotope analysis.

Stable isotope analysis: Fish eye lens tissue was processed for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis (SIA) as a tool for determining trophic position ($\delta^{15}N$) and basal resource use ($\delta^{13}C$). We performed the dissection, or delamination, of eye lenses using a light microscope with an ocular micrometer and high precision forceps. Laminae were dissected from the lens and prepared for SIA while measuring the lens diameter between each delamination (see Fig. 1.2a). We identified eye lens layers by volumetric midpoint rather than radial midpoint because the volumetric midpoint more accurately describes the contribution of tissue to the stable isotope value (i.e., 50% of the tissue by volume falls “before and “after” the volumetric midpoint).

Tissue samples included eye lens, fish dorsal white muscle, macroinvertebrate, and plants. These samples were prepared by drying in an oven at 55° C for 24-48 hours, then crushing and homogenizing. Approximately 0.5 mg of animal tissue or 1.1 mg of plant tissue were packed into tin capsules. Due to low sample mass, eye lens tissue samples were often near 0.2 mg, but this was within the acceptable C and N range for the instrument used. We analyzed samples using an Elemental Analyzer (NA 2500; CE Instruments, Wigan, United Kingdom) interfaced with a Delta V Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts) at the University of Washington, referenced to 2 glutamic acid standards and Bristol Bay Sockeye Salmon (*Oncorhynchus nerka*). Accuracy and precision were calculated based on the known isotopic values of the standards and the repeated measurements of standard samples throughout each sample sequence. The average nitrogen accuracy and precision across all sample sequences were 0.06‰ and 0.14‰, respectively. Average carbon accuracy and precision across all sample sequences were 0.07‰ and 0.05‰, respectively.

Stable isotope ratio data are reported in permil (‰) units as the delta (δ), or relative difference, from a standard as follows: $\delta X = ((R_{sample}/R_{standard}) - 1) * 1000$ where X represents ^{13}C or ^{15}N and R represents the ratio of heavy to light isotope for each element (i.e., $^{13}C/^{12}C$ or $^{15}N/^{14}N$). When comparing data across the entire food web, the $R_{standard}$ was Vienna Pee Dee Belemnite (VPDB) for ^{13}C and atmospheric ^{15}N. Further analyses of fish tissue data referenced $\delta^{13}C$ and $\delta^{15}N$ to Physidae snails collected at each site as an isotopic baseline to allow for comparisons between sites (Appendix 1: Table A1.1). Physidae snails are an appropriate baseline organism because they were present at all sites and show relatively slow tissue turnover rates (Post 2002; Jardine et al. 2014). 6/9/25 3:08:00 PMWe expect little change in temporal baseline stable isotope values due to the short length of time included in our eye lens comparisons (< 6 years). This is supported by a comparison to previously collected macroinvertebrate stable isotope data from 2016 (Rogosch and Olden 2020) where we found variable, but largely overlapping isotopic niches for three taxa between the two years (Appendix 1: Figure S1.1).

We confirmed eye lens suitability for trophic analysis in these species by (1) constructing the fish length – lens diameter relationship for each species, (2) comparing $\delta^{13}C$ and $\delta^{15}N$ values between eye lens and muscle tissue, and (3) testing for consistency between $\delta^{13}C$ and $\delta^{15}N$ values of different eyes of the same individual fish (Quaeck-Davies et al. 2018; Young et al. 2022). Linear regression models were used to quantify the species-specific relationships between fish length and eye lens diameter. The relationship between stable isotope values of muscle tissue and the outer eye lens tissue was also evaluated using a linear regression model for each stable isotope, $\delta^{13}C$ and $\delta^{15}N$. We tested for the effect of fish age on the difference between muscle and outer eye lens tissue stable isotope values using an ANOVA. Lastly, a comparison between left and right eye lens $\delta^{13}C$ and $\delta^{15}N$ values was performed for select fish using an ANCOVA (α = 0.05 for both tests).

Fish aging: We extracted otoliths from all dissected fish for aging analysis. The sagittal otoliths are used for aging in typical teleosts, whereas lapillar otoliths were used to age ostariophysans (e.g., suckers, see Fig. 1.2b) because of their readability and conservative growth (Hoff, Logan, and Markle 1997). Following the protocols outlined in Chittaro et al. (2020), otoliths were mounted using Crystalbond onto a microscope slide, then polished using deionized water and wet/dry sandpaper to expose the nuclei and edge increments. Next, otoliths were imaged using a compound microscope and ImagePro software. In some cases where otoliths were damaged during the polishing process or difficult to read, the second otolith was also polished. Each author aged the otoliths separately, using random numbers assigned to each individual fish without knowledge of length or site. Aging estimates were evaluated by percent agreement and among-reader precision (Quist et al. 2007). Where disagreements arose, authors met to decide on final estimates. First-time age estimates produced 86% agreement between readers for all six species. Of the initial disagreements, 76% were within one year. Among reader precision was

4.8, calculated as the coefficient of variation (CV) for each individual fish, then averaged. Sample size and ages of fish by species and community type are provided in Appendix 1: Table A1.2. Distances from the core to each otolith annulus were measured using ImageJ along a consistent radius line for each species.

Statistical analysis: We inferred lifetime trophic trajectories of individual fish by analyzing $\delta^{13}C$ and $\delta^{15}N$ values in isotopic niche space. The direction and magnitude of change in $\delta^{13}C$ and $\delta^{15}N$ between pairs of adjacent eye lens layers defined the trophic trajectory of individual fish (on a $\delta^{13}C$ and $\delta^{15}N$ biplot where $x = \delta^{13}C$ and $y = \delta^{15}N$; Schmidt et al. 2007). The average lifetime trophic trajectory of a single fish is the mean angle and net change between eye lens layers in $\delta^{13}C$ and $\delta^{15}N$. The Rayleigh test for unimodal departures from uniformity was used to determine whether individual mean angle clustering was significantly non-random. Watson's two-sample test of homogeneity was used to test whether the species mean of individual mean angles between pairs of community types differed significantly ($\alpha = 0.05$ for both tests). To facilitate comparisons, sites were classified as "native-only" and "mixed assemblage" of both native and nonnative species, and within the mixed assemblage sites, they were further classified as "native dominated" and "nonnative dominated" based on abundance (catch) data (Fig. 1).

Lifetime trophic trajectories were compared between species and community types using the following metrics: net change ratio, directionality, and intraspecific trajectory variability (Sturbois et al. 2022). Net change ratio describes the ratio of overall change to total path length (excluding fish with <3 eye lens layers). A high net change ratio signifies that a high proportion of the trajectory path contributes to overall changes and suggests that drivers of ecological dynamics are relatively consistent. Directionality describes the consistency with which an individual follows the same direction on a scale from near 0 (meandering) to 1 (straight path). High directionality indicates high stability of ecological drivers (e.g., prey availability, species interactions) that contribute to the individual trophic trajectory. Intraspecific variability of centered trajectories were measured using directed segment path dissimilarity, which represents the resemblance between trajectories. This metric was applied to each pair of individuals within a species and community type, then averaged. Circular and trajectory statistics were calculated in R using the "circular" (Agostinelli and Lund 2023) and "ecotraj" (De Cáceres et al. 2019) packages, respectively. All analyses were performed with R version 4.4.0 (R Core Team 2024).

Age at each eye lens layer was calculated from linear regression models of eye lens diameter and otolith radius vs. fish length, coupled with otolith annuli measurements for each individual fish. Uncertainty in estimates was incorporated using bootstrapping of the linear regression models. Fish length at the volumetric midpoint of each eye lens layer was first estimated using the linear model predicting total length from lens diameter for each species with bootstrapping (1000 iterations) to account for uncertainty in estimates. The strong relationship between eye lens diameter and total length has been documented with high R^2 values for many fish species (Tzadik et al. 2017; Quaeck-Davies et al. 2018). Next, the otolith radius at each eye lens layer was estimated from individual linear models of the Fraser-Lee biological intercept (otolith radius at length 0) and measurements at time of capture for each fish, with bootstrapping (1000 iterations) of the biological intercept based on the otolith radius vs. fish length linear models. Lastly, age at each eye lens layer, measured in years, was then estimated from length-at-age back-calculation methods based on otolith annuli growth measurements for each individual fish (Quist, Pegg, and DeVries 2012). Additional details on the back-calculation methods are provided in Appendix 1.

Stable isotope time series were created for individual fish using eye lens tissue stable isotope values and age at eye lens layer estimates. Linear mixed-effects models were applied to these time series to examine changes in $\delta^{13}C$ and $\delta^{15}N$ through time and compare these changes between community types. These analyses were performed separately for each species, using eye lens layer age and community type as fixed factors, with an interaction term. Nested random effects of site and fish were included with respect to the intercept. Autocorrelation of lag-1 was included due to temporal autocorrelation. All data met the assumptions of linear relationships and homoscedasticity of residuals. Individual trophic trajectories were split into ontogenetic stages, young of the year (≤1 year, YOY) and adult (>1 year), based on estimated ages at each eye lens layer, then compared between community types within each species. Due to the variable lengths of individual time series, especially concentrated in younger individuals, we decided to summarize the time series using trajectory metrics (see above), rather than formal time series analyses.

1.4 RESULTS

Stable isotope analysis of food web structure revealed overall increases in δ^{13}C and δ^{15}N from primary producers to secondary consumers (Fig. 1.3). In the presence of nonnative fishes, we report marked displacement of native fish lifetime trophic trajectories. Lifetime trophic trajectories of native fishes displayed decreases of δ^{13}C and δ^{15}N in mixed community sites relative to native-only sites, demonstrated by mean angles shifting counterclockwise in C-N circular histograms (Fig. 1.4 a-c, Table 1.1). By contrast, nonnative green sunfish and bullhead showed consistent increases in δ^{13}C and δ^{15}N regardless of the fish community (Fig. 1.4 d-e, Table 1.1). Most population trajectories were directionally significant (Rayleigh's test $p < 0.05$), with the exception of Sonora sucker and desert sucker in native-only sites. Within species, the mean angle of lifetime trophic trajectories were highly variable; species means were not significantly different between community types (Watson's test $p > 0.05$). These trajectories originated from overlapping core eye lens isotopic niches across sites (Appendix 1: Fig. A1.2), and therefore observed differences in trophic trajectories are reflective of different end points (i.e., trajectories are diverging rather than converging).

Native species were more coordinated in their lifetime trophic trajectories in the presence of nonnative species relative to the absence of nonnative species, as evidenced by lower trajectory dissimilarity (i.e., higher similarity) for all native species in mixed communities compared to native-only communities (Table 1.1). The average magnitude of net change in δ^{15}N was lower, on average, for native fishes that were members of mixed communities when compared to native-only communities (differences: roundtail chub -0.09‰, Sonora sucker -0.44‰, desert sucker -0.74‰). For nonnative species, the difference between net change in δ^{15}N from native-dominated to nonnative-dominated communities was variable (differences: green sunfish -0.14‰, bullhead spp. +1.34‰). However, when comparing species, the lifetime increase in δ^{15}N was consistently higher for nonnative species (ranging from 0.98 to 2.38‰) compared to native species (maximum of 0.89‰). This pattern was evident in δ^{13}C lifetime trajectories as well (Table 1.1). Roundtail chub, in particular, showed the greatest decrease of net change in δ^{13}C (-1.47‰ difference) when in the presence of nonnative species in mixed communities compared to native-only communities.

Trajectory metrics reveal species-specific lifetime responses within different community types (Table 1.1). The mean net change ratio for Sonora sucker was much larger (0.65; on a scale from 0 to 1) in native-only communities when compared to mixed communities (0.37), implying that their lifetime trophic trajectory traced a more direct path due to more consistent ecological drivers of trophic ecology. Sonora sucker displayed higher circular variance in the presence of nonnative species (25.7° in native-only, 40.0° in mixed communities). Circular variance in mean angle for roundtail chub and desert sucker, however, were remarkably consistent between community types. Directionality was similar across species regardless of community type, with means ranging from 0.43 to 0.64 (on a scale from 0 to 1).

Lifetime trophic trajectory displacement of native species, represented by the difference in mean angle, is largely evident in the first year of life (Table 1.2). Lifetime trophic trajectories showed significant decreases in $\delta^{13}C$ and $\delta^{15}N$ for YOY roundtail chub and desert sucker in mixed communities in comparison to native-only communities (Table 1.2). Trophic trajectories in adult years, however, showed no such differences between community types for all native species, with individuals generally becoming more enriched in ^{15}N with age (Table 1.2). By contrast, nonnative species displayed more consistent trophic trajectories when comparing YOY and adults (Table 1.2). Lifetime trophic trajectories of YOY green sunfish and both YOY and adult stages of bullhead showed increasing $\delta^{15}N$ across ontogeny, whereas adult green sunfish trajectories in nonnative-dominated communities showed slight decreases in $\delta^{15}N$ over time (Table 1.2).

Mapping lifetime trophic trajectories onto the common scale of time (as opposed to eye lens diameter) strengthens the above trajectory analysis by allowing comparison of the rate of isotopic change between community types. For roundtail chub, the presence of nonnative species led to a significantly greater decrease in $\delta^{13}C$, but similar increase in $\delta^{15}N$ over time, relative to native-only communities (Fig. 1.5a). Sonora sucker trophic trajectories consistently decreased in $\delta^{13}C$ and increased in $\delta^{15}N$ over time (Fig. 1.5b). Desert sucker trophic trajectories decreased in $\delta^{13}C$ over time to a significantly greater degree in mixed communities (Fig. 1.5c). Although not a statistically significant interaction between fish age and community type, desert sucker decreased in $\delta^{15}N$ over time in mixed communities but increased in $\delta^{15}N$ over time in native-only sites. Green sunfish displayed consistent increases in $\delta^{13}C$ and $\delta^{15}N$ over time, without an impact of community type on lifetime rates of trophic change (Fig. 1.5d). The difference in $\delta^{15}N$ rate of increase for bullhead spp. in nonnative-dominated sites was significantly greater relative to native-dominated sites, but the $\delta^{13}C$ rate of change showed no significant difference based on community type (Fig. 1.5e).

We addressed the uncertainties associated with using eye lens tissue for trophic ecology analysis (Quaeck-Davies et al. 2018). Species-specific relationships between eye lens cortex diameter and fish total length was confirmed to be strongly linear with R^2 values greater than 0.85 for each species (Appendix 1: Fig. A1.3). The comparison between muscle tissue and outer eye lens tissue stable isotopes (excluding fish without multiple eye lens layers) revealed a positive relationship between the two tissue types (Appendix 1: Fig. A1.4). The difference between stable isotope values of muscle and outer eye lens tissue (calculated as eye SIA – muscle SIA) ranged from -5.96 to 6.96‰ for $\delta^{13}C$ and between -5.93 to 4.40‰ for $\delta^{15}N$. We found that fish age had a significant effect on the difference between eye and muscle stable isotopes values (ANOVA; $\delta^{13}C$: $F_{[1,265]} = 15.52$, $p < 0.05$; $\delta^{15}N$: $F_{[1,265]} = 46.84$, $p < 0.05$), although the effect was opposite between the two stable isotopes. The outer eye lens $\delta^{13}C$ values were on average 1.47‰ higher than muscle tissue for age 1 fish, but the outer eye lens $\delta^{15}N$ values were on average 2.59‰ lower relative to muscle tissue for age 1 fish. As fish age, the difference approached zero. This is likely because the outer eye lens layers of larger fish include more tissue and can be separated into smaller time periods more closely aligning with muscle tissue stable isotope integration time (i.e., 1-2 months). There was no significant effect of using the right vs. left eye on $\delta^{13}C$ and $\delta^{15}N$ values (ANCOVA; $\delta^{13}C$: $F_{[1,139]} = 0.020$, $p > 0.05$; $\delta^{15}N$: $F_{[1,139]} = 0.066$, $p > 0.05$; Appendix 1: Fig. A1.5).

1.5 DISCUSSION

Biological interactions between and among species manifest across the entire lifespan of an organism. However, the range of potential effects on trophic ecology through time has been rarely captured in past research. Our study is the first to integrate individual aging techniques (here, otolith growth measurements) with stable isotope values of fish eye lens tissue to reconstruct lifetime trophic trajectories of multiple fish species, allowing for comparisons across species and community assemblages. These results reveal the prolonged impacts that invasive fishes have on the lifetime trophic ecology of native fishes, including ontogenetic dietary shifts, with implications for native species population growth and persistence.

Native fishes displayed consistent displacement of their lifetime trophic trajectory in sympatry with nonnative species, relative to native-only communities. In the presence of nonnative fishes, native individuals assimilated resources more depleted in ^{15}N and ^{13}C, as evidenced by lower δ^{15}N and δ^{13}C values, suggesting a lower trophic level and more reliance on aquatic rather than terrestrial derived resources, respectively. The fact that we observed this for all three native species is noteworthy due to the diverse dietary habits of the native fishes studied. Nonnative fishes have been previously shown to competitively exclude native fishes from consuming terrestrial resources (Baxter et al. 2004; Yonekura et al. 2009) and displace native fishes to lower trophic positions (Vander Zanden, Casselman, and Rasmussen 1999; Marks et al. 2010; Rogosch and Olden 2020).

Nested within the broad native fish community patterns was substantial interspecific variation in trophic trajectories, reflecting the complexity of outcomes resulting from species interactions occurring over the lifetime of an individual. Roundtail chub in mixed native-nonnative communities displayed the largest lifetime trophic displacement to depleted ^{13}C values relative to native-only sites and a significant decrease in the rate of δ^{13}C increase over time. This is likely due to their high dietary similarity with the nonnative green sunfish and bullhead throughout their lifetime. Desert sucker trophic trajectories reflected the greatest displacement to depleted ^{15}N and decrease in δ^{15}N rate of change over time, indicating a larger decrease in trophic level through ontogeny. The displacement of Sonora sucker trophic trajectories was moderate with respect to δ^{13}C and δ^{15}N. In the San Rafael River, Utah, roundtail chub and two native sucker species exhibited divergent trophic responses in mixed, compared to native-only, communities, as measured by fin clip SIA capturing a single point in time (Walsworth, Budy, and Thiede 2013). Mixed communities of the San Rafael River are composed of more nonnative species than those found in Burro Creek, including channel catfish, sand shiner, and white sucker. Within this more densely occupied trophic space, roundtail chub displayed a wider range of isotopic values, on average higher in δ^{15}N compared to native-only sites (Walsworth, Budy, and Thiede 2013), perhaps reflecting antagonistic impacts of multiple nonnative species (Jackson 2015). Biotic interactions, from exploitative and interference competition (David et al. 2017) to predator avoidance (Lima 1998), may be responsible for changes in lifetime trophic ecology based on community composition.

Nonnative fishes exhibited lifetime trophic trajectories that were relatively consistent in both native- and nonnative-dominated communities. Such patterns likely arise from strong asymmetric competition between native and nonnatives fishes, an emerging reality in dryland rivers of the southwestern United States (Rogosch and Olden 2020; George and Collins 2024). However, a closer examination revealed that trophic trajectories for nonnative green sunfish differed according to age. Unlike the trophic trajectories of YOY green sunfish that did not differ between community types, the trophic trajectories of adults shifted to lower δ^{15}N values in nonnative-dominated communities, suggesting that elevated intraspecific interactions and interspecific interactions with other nonnative species limited green sunfish to a lower trophic level. These patterns highlight the plasticity of green sunfish feeding habits in response to community composition; a characteristic of other highly successful invasive freshwater fishes (Pettitt-Wade et al. 2015; Rolla, Consuegra, and Garcia De Leaniz 2020; Glassic et al. 2023; Mpopetsi and Kadye 2024). Such patterns also point to the growing recognition of multiple invaders having antagonistic interactions at specific ontogenetic stages (Jackson 2015; Bissattini et al. 2021).

We recognize a number of key assumptions when applying stable isotopes to track the trophic ecology of individuals over time. First, we assume that fish movement is fairly limited, and therefore individuals are not mixing among community types; an assumption supported by the distance between study sites and flow intermittency that leads to seasonal or permanent fragmentation in the Burro Creek basin. Second, differences in the carbon and nitrogen stable isotope spatial baseline were standardized by referencing fish eye lens tissue to Physidae snail ^{13}C/^{12}C and ^{15}N/^{14}N ratios at each site. Third, we assume a relatively stable temporal baseline over the course of fish lifetimes (maximum 6 years), with macroinvertebrate stable isotope data from the same sites in 2016 vs. 2021 indicating variable but overlapping isotopic niches (Appendix 1: Fig. A1.1). Close proximity of sites over land leads us to assume adequate dispersal of most macroinvertebrates between sites and consistent environmental conditions, creating similar isotopic variation in food sources across sites. Although stable isotope baseline values will vary through time, snails have a tissue turnover stable isotope half-life of 20-50 days, longer than autochthonous primary producers or other common macroinvertebrates in the region (Jardine et al. 2014), which have been previously used to correct for spatial baseline variation (Rogosch and Olden 2020). Fourth, fish sampling resulted in unequal sample sizes and age structures for species between community types, which may impact our interpretation of lifetime trophic trajectories.

Displacement of lifetime trophic trajectories of individuals may scale-up to population level consequences through reductions in growth, survival, and recruitment (Olson 1996; Post 2003; Huss, Byström, and Persson 2008). Our results show a clear displacement of native fish lifetime trophic trajectories in the presence of nonnative fishes, which may lead to depressed growth rates and further threaten the persistence of native species vulnerable to nonnative gape-limited predators. Competition through aggressive dominance or exploitation of a shared resource may alter ontogenetic dietary shifts and negatively impact individual fish growth (Marchetti 1999; Baxter et al. 2007; Houde, Wilson, and Neff 2015; Britton et al. 2018), although native species growth was not reduced in the San Rafael River despite high isotopic niche overlap with nonnative species (Walsworth, Budy, and Thiede 2013). Predator avoidance, a non-consumptive effect, has altered feeding habits resulting in reduced growth of prey species (Werner et al. 1983; Peckarsky et al. 1993). The threat of gape-limited predators creates a trade-off for prey between elevated predation risk and optimal foraging to increase growth and body size to avoid gape-limited predators (Heck 2006; Urban 2007). For example, juvenile Eurasian perch responded to gape-limited predators by changing habitat use from open water to macrophyte vegetation, leading to decreased feeding and growth; a response not observed for larger age 1+ perch (Diehl and Eklov 1995). Altered ontogenetic dietary shifts may result in slower growth and reduced reproduction, impacting species persistence (Sánchez-Hernández et al. 2019). Impacts to individual trophic ecology can also have ecosystem effects, because native species may not be fulfilling the same trophic niche when co-occurring with nonnative species (Kindinger and Albins 2017; Leal et al. 2021).

Intraspecific variability in ontogenetic dietary shifts has been recognized as an emerging research need (Sánchez-Hernández et al. 2019). Here, we found evidence for intraspecific variability in lifetime trophic trajectories of native species, the magnitude of which differed among species and in relation to the presence of nonnative fishes. Variability in individual trophic trajectories reflects behavioral plasticity in response to variation in prey availability, competition, or predation (Araújo, Bolnick, and Layman 2011; Latli et al. 2019). The presence of nonnative species was associated with greater intraspecific variation in trophic trajectories for Sonora sucker, counter to our prediction that omnivorous roundtail chub would express more trophic plasticity. This may be a result of roundtail chub displaced from consuming preferred prey due to competition with the nonnative species, but feeding within a similarly sized trophic niche between native-only and mixed native-nonnative communities. Also omnivorous, Sonora sucker were able to expand their isotopic niche when overlapping in space with nonnative species. Recent years have witnessed a shift in attention towards better understanding the patterns and drivers of intraspecific variability in behavioral and trophic ecology, and quantifying the effects of this intraspecific variability on food web and ecosystem dynamics (Zhao et al. 2014; Zandonà et al. 2017; Raffard et al. 2019). Our study advances these efforts by documenting how species invasions can affect both intra- and inter-specific trophic variability in native species.

Fish eye lens stable isotope analysis provides an opportunity to study lifelong trophic interactions and retrospectively link individual trophic trajectories to specific ages throughout ontogeny. Previous studies have attempted to measure longer dietary time frames by combining multiple tissue types with varying isotopic turnover rates (Vander Zanden et al. 2015; Wyatt et al. 2019; Skinner et al. 2022), though these methods are limited by uncertainty in turnover and fractionation rates between tissues. This study estimated age at eye lens layers using otoliths, thus allowing for time-referenced trophic comparisons between species and across space. Previous studies have compared inter-individual trophic trajectories using estimated fish length as a comparable metric (Quaeck-Davies et al. 2018; Young et al. 2022; Vecchio and Peebles 2022), which fails to account for considerable variability in length at age for fishes. Our novel approach estimated age at each eye lens layer by linking two fundamental allometric relationships: first, eye lens diameter and fish length, and second, fish length and otolith radius. This was made possible due the indeterminate growth of these species and a sampling regime that captured fish across a range of ages (and lengths). Otoliths and eye lens layers have been jointly examined to track mercury uptake (Miraly et al. 2022) and element concentrations (Stounberg et al. 2022), but this is the first application to community trophic ecology.

Our results reveal the importance of understanding lifetime trophic impacts for the benefit of basic ecological knowledge, native species conservation, and management action evaluation. Fish eye lens trophic trajectories present a novel approach for measuring intraspecific variability, leading to a greater understanding of how that variation influences community structure and ecosystem function (Bolnick et al. 2011; Des Roches et al. 2017). Both biotic and abiotic factors interact with intraspecific variability in complex ways (Raffard et al. 2020). Stressors such as invasive species, habitat degradation, and global climate change threaten native species inconsistently throughout ontogeny (Pandori and Sorte 2019; Crozier and Siegel 2023). Therefore, understanding the specific ontogenetic impacts of these stressors will lead to more successful native species conservation efforts. Following management actions, trophic trajectories can be used as a metric to evaluate community restoration. Trophic niche recovery has been documented for native species following the removal of aquatic invasive species (Lepak, Kraft, and Weidel 2006; Rogosch and Olden 2020; O'Hea Miller et al. 2023) and community recovery after habitat degradation (Dawson et al. 2024). Uncovering lifetime trophic trajectories leads to a more comprehensive picture of individual and community trophic ecology.

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1.8 TABLES

Table 1.1: Trophic trajectory metrics reported by species and community type for fish captured in Burro Creek basin, Arizona. Individual trophic trajectories were constructed from fish eye stable isotope (δ^{13}C and δ^{15}N) time series and plotted in C-N circular space.

Species	**Community Type**	**Mean Angle (°)**	**Circular Var (°)**	**Net Change in δ^{13}C (‰)**	**Net Change in δ^{15}N (‰)**	**Net Change Ratio**	**Directionality**	**Dissimilarity (‰)**
Roundtail Chub	Native-only	**0.8**	30.2	-0.04	0.89	0.52	0.45	2.08
	Mixed	**302.5**	30.2	-1.51	0.80	0.55	0.50	1.96
Sonora Sucker	Native-only	30.3	25.7	0.10	0.70	0.65	0.54	2.81
	Mixed	**321.3**	40.0	-0.46	0.26	0.37	0.46	2.23
Desert Sucker	Native-only	306.9	38.0	-0.77	0.30	0.57	0.57	3.19
	Mixed	**246.3**	38.0	-1.20	-0.44	0.48	0.43	2.30
Green Sunfish	Native-Dom	**35.5**	29.5	1.09	1.12	0.70	0.60	1.80
	Nonnative-Dom	**11.0**	35.1	0.42	0.98	0.49	0.48	2.19
Bullhead spp.	Native-Dom	**24.6**	20.2	0.36	1.04	0.52	0.48	1.77
	Nonnative-Dom	**6.7**	8.7	0.79	2.38	0.81	0.64	1.98

Notes: Columns Net Change in ^{13}C through Dissimilarity represent the mean for each species and community type. Bolded mean angles represent unimodal departures from uniformity (Rayleigh's $P < 0.05$).

Table 1.2: Mean angle (with circular variation), in degree units, of trophic trajectories reported by life stage of each species and community type for fish captured in Burro Creek basin, Arizona. Individual trophic trajectories were constructed from fish eye stable isotope (δ^{13}C and δ^{15}N) time series and plotted in C-N circular space.

Species	**Young-of-the-year**			**Adult**		
Native	Native-only	Mixed	Difference	Native-only	Mixed	Difference
Roundtail Chub	22.2 (38.8)	279.3 (28.6)	**-102.9**	359.2 (37.3)	1.5 (36.9)	2.3
Sonora Sucker	65.0 (46.2)	250.0 (45.7)	-175.0	330.2 (4.4)	356.8 (22.4)	26.6
Desert Sucker	266.7 (38.7)	226.7 (15.9)	**-40.0**	13.7 (32.8)	42.7 (33.4)	29.0
Nonnative	Native-Dom	Nonnative-Dom	Difference	Native-Dom	Nonnative-Dom	Difference
Green Sunfish	40.3 (31.1)	14.5 (31.3)	-25.8	28.9 (15.8)	103.6 (27.4)	**74.7**
Bullhead spp.	61.0 (24.8)	354.5 (12.4)	**-66.5**	348.8 (13.1)	357.2 (3.2)	8.4

Notes: Difference between mean angle bolded when significant (Watson's two-sample test of homogeneity: $P < 0.05$). An angle of 0° or 360° corresponds to a vertical vector pointing up from the origin, representing an increase in δ^{15}N (180 indicates a decrease in δ^{15}N) and no change in δ^{13}C. An angle of 90° corresponds to a horizonal vector pointing to the right from the origin, representing an increase in δ^{13}C (270° indicates a decrease in δ^{13}C) and no change in δ^{15}N.

1.9 FIGURES

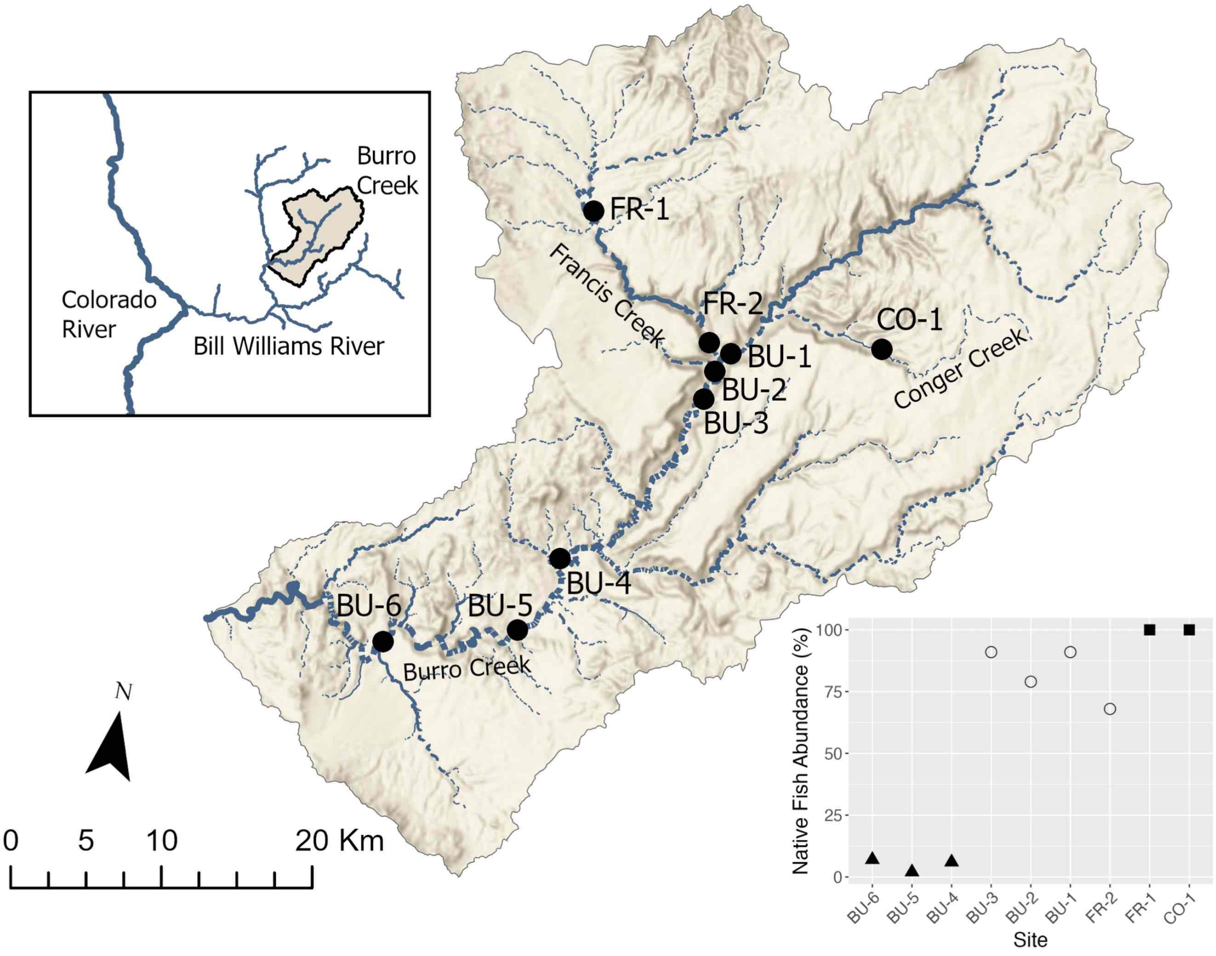

Figure 1.1: Map of Burro Creek watershed with sampling locations (dotted lines are intermittent stream sections and solid lines are perennial). Upper left inset shows the Bill Williams River with the Burro Creek Basin in light brown. Lower right inset shows invasion gradient across sites according to percent of native individuals in catch (downstream on the left, upstream on the right). Within the lower right inset, solid circles represent nonnative-dominated mixed sites, open circles represent native-dominated mixed sites, and closed squares represent native-only sites.

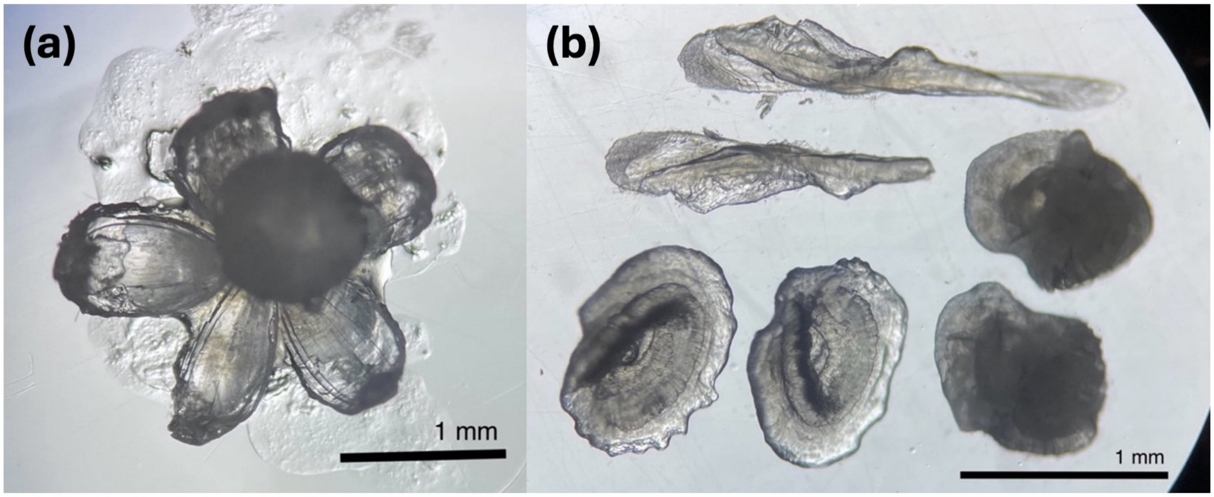

Figure 1.2: Fish eye lens delamination under the microscope (a) and desert sucker otoliths clockwise from top: sagittae (smaller one is broken), lapilli, and asterisci (b). Photo credit: Jessica Diallo.

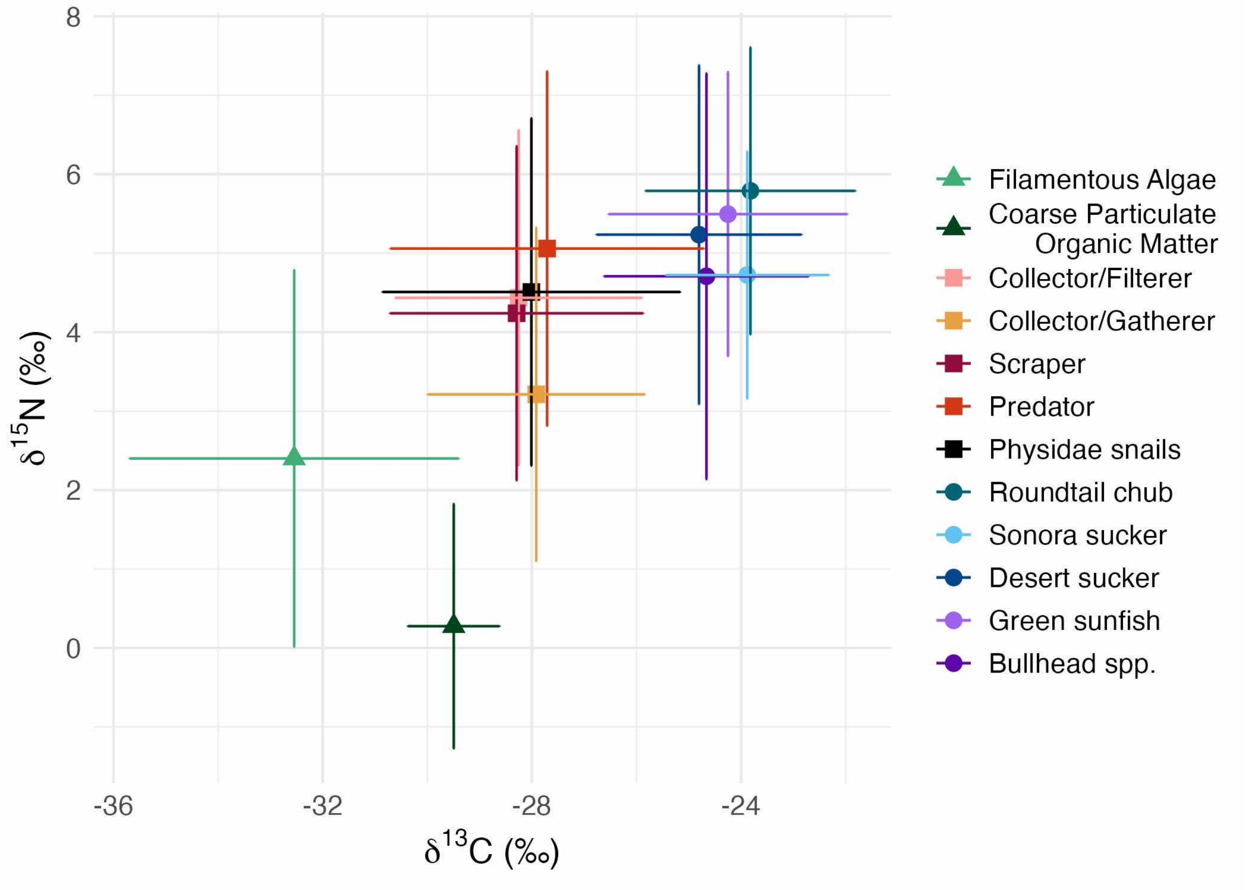

Figure 1.3: Stable isotope biplot displaying the food web structure in Burro Creek, AZ. The mean across sites is displayed with standard deviation error bars. Primary producers are filamentous algae (aquatic derived) and coarse particular organic matter (terrestrial derived). Aquatic macroinvertebrate stable isotope values are separated by functional feeding group for the 10 most common families: collector/filterer (Simuliidae, Philopotamidae), collector/gatherer (Baetidae, Chironomidae, Leptohyphidae), scraper (Heptageniidae, Physidae), and predator (Coenagrionidae, Corydalidae, Tabanidae). Physidae snails are also displayed separately as the stable isotope baseline used to standardize fish eye lens values across sites. Fish eye lens tissue is used to represent the different fish species (lens stable isotope data first averaged within individuals, then each site). Units are per mil relative to international standards (VPBD for $\delta^{13}C$ and air for $\delta^{15}N$).

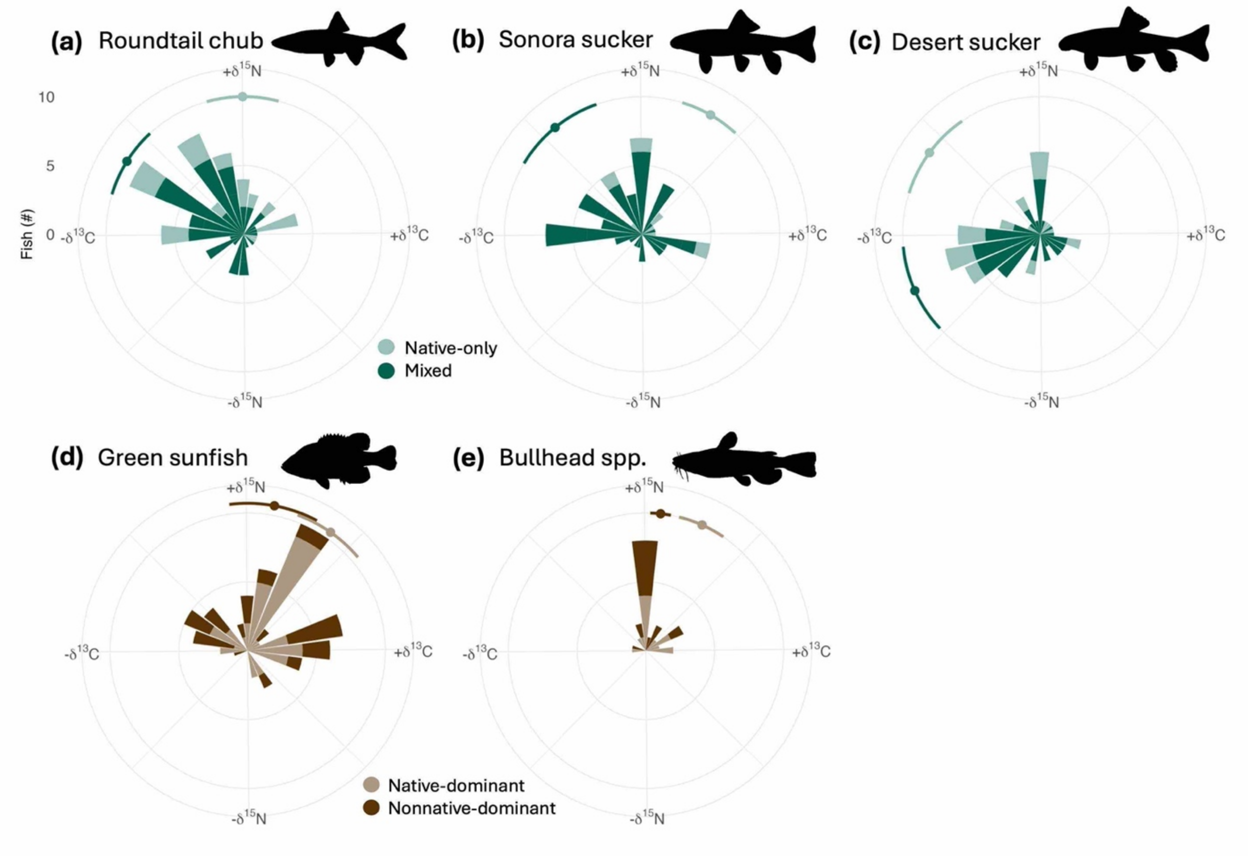

Figure 1.4: Lifetime trophic trajectory circular histograms of native fish in native only (light green) and mixed community sites (dark green), and nonnative fish in native-dominant (light brown) and nonnative-dominant fish communities (dark brown) of Burro Creek, AZ. Species include roundtail chub (a), Sonora sucker (b), desert sucker (c), green sunfish (d), and bullhead spp. (e). Directional mean (point) and circular variance (arc on circumference) are displayed for each species and community type. Units are per mil relative to Physidae snail spatial baseline.

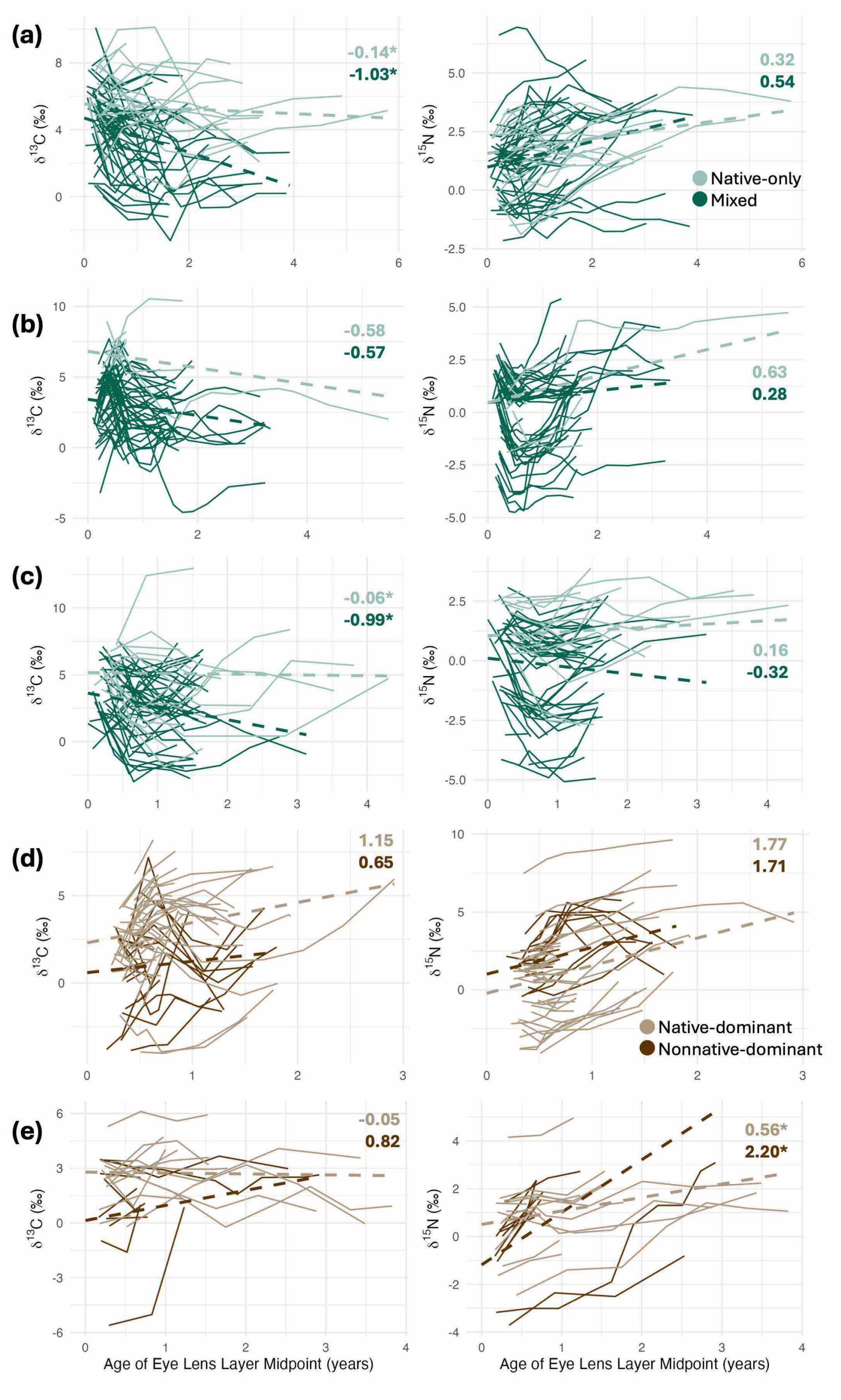

Figure 1.5: Temporal changes in $\delta^{13}C$ (left) and $\delta^{15}N$ (right) of individual fish of Burro Creek, AZ separated by species and community type. Species include roundtail

chub (a), Sonora sucker (b), desert sucker (c), green sunfish (d), and bullhead spp. (e). Dotted lines display the results of linear mixed effects models. Numbers on the right side of each plot display the slope of each linear model (units are per mil per year), with stars indicating a significant interaction between eye lens layer age and community type ($P < 0.05$). Units are per mil relative to Physidae snail spatial baseline.

1.10 APPENDIX 1

Table A1.1: Physidae snail baseline stable isotope ratios at each sampling location in Burro Creek, Arizona.

Sampling Location	**Nested Site**	**$^{13}C/^{12}C$**	**$^{15}N/^{14}N$**
CO-1	site 1	0.0108477	0.0036964
	site 2	0.0108318	0.0037012
FR-1	site 1	0.0108044	0.0036993
	site 2	0.0108428	0.0036871
FR-2	site 1	0.0108930	0.0037016
	site 2	0.0109126	0.0037034
BU-1		0.0108670	0.0036834
BU-2		0.0108807	0.0036935
BU-3		0.0108903	0.0036839
BU-4		0.0108933	0.0036846
BU-5		0.0108491	0.0036832
BU-6		0.0108896	0.0036994

Table A1.2: Number of fish included in the analyses, divided by species, community type, and age.

Species	**Community Type**	**Age**					
		1	**2**	**3**	**4**	**5**	**6**
Roundtail chub	Native-only	2	1	4	9	1	1
	Mixed	13	28	0	12	0	0
Sonora sucker	Native-only	5	2	0	0	0	1
	Mixed	12	30	1	6	0	0
Desert sucker	Native-only	9	7	1	3	2	0
	Mixed	6	37	0	2	0	0
Green sunfish	Native Dominated	33	14	1	0	0	0
	Nonnative Dominated	23	10	0	0	0	0
Bullhead spp.	Native Dominated	2	8	0	4	0	0
	Nonnative Dominated	19	1	2	0	0	0

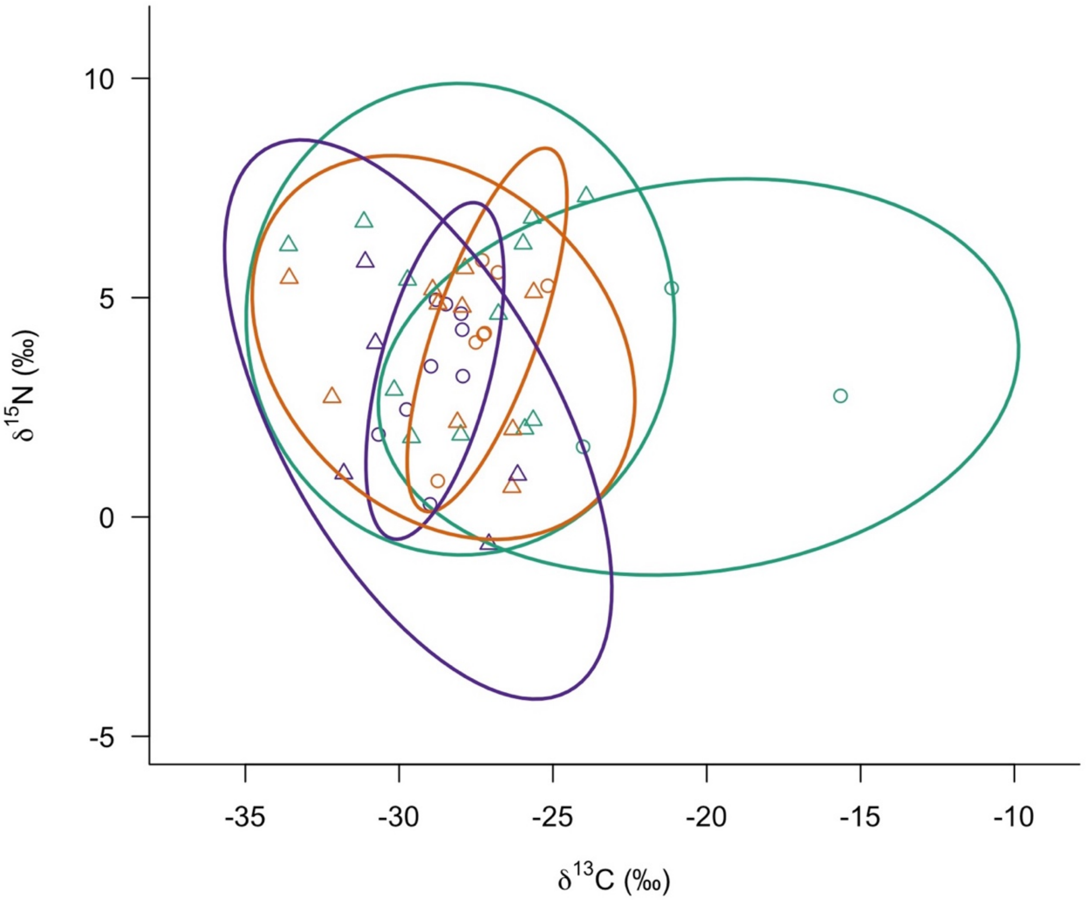

Figure A1.1: Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) and prediction ellipses (95% confidence level) of macroinvertebrates in Burro Creek, Arizona, between 2016 (circles) and 2021 (triangles). Macroinvertebrate families displayed are Simuliidae larvae (orange), Baetidae larvae (purple), and Physidae snails (green). Units are per mil relative to international standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and air for $\delta^{15}N$).

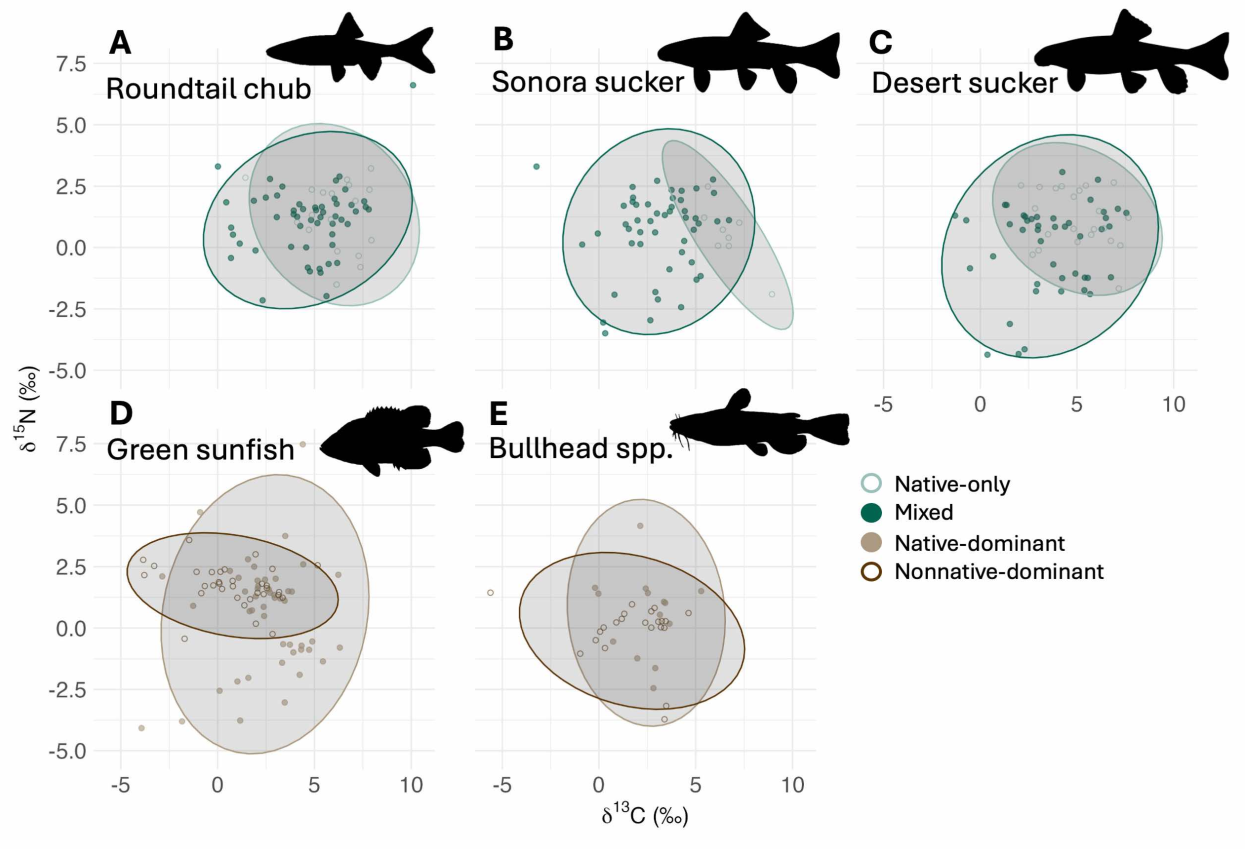

Figure A1.2: Stable isotope values (δ^{13}C and δ^{15}N) and prediction ellipses (95% confidence level) of core eye lens layer for each species: roundtail chub (A), Sonora sucker (B), desert sucker (C), green sunfish (D), and bullhead spp. (E) in Burro Creek, Arizona. The proportion of overlap in maximum likelihood prediction ellipses was calculated as 0.65 (roundtail chub), 0.17 (Sonora sucker), 0.50 (desert sucker), 0.29 (green sunfish), and 0.58 (bullhead spp.) using the SIBER package (Jackson and Parnell, 2023). Units are per mil relative to Physidae snail spatial baseline.

Jackson, A. L. and A. C. Parnell. 2023. SIBER: Stable Isotope Bayesian Ellipses in R. R.

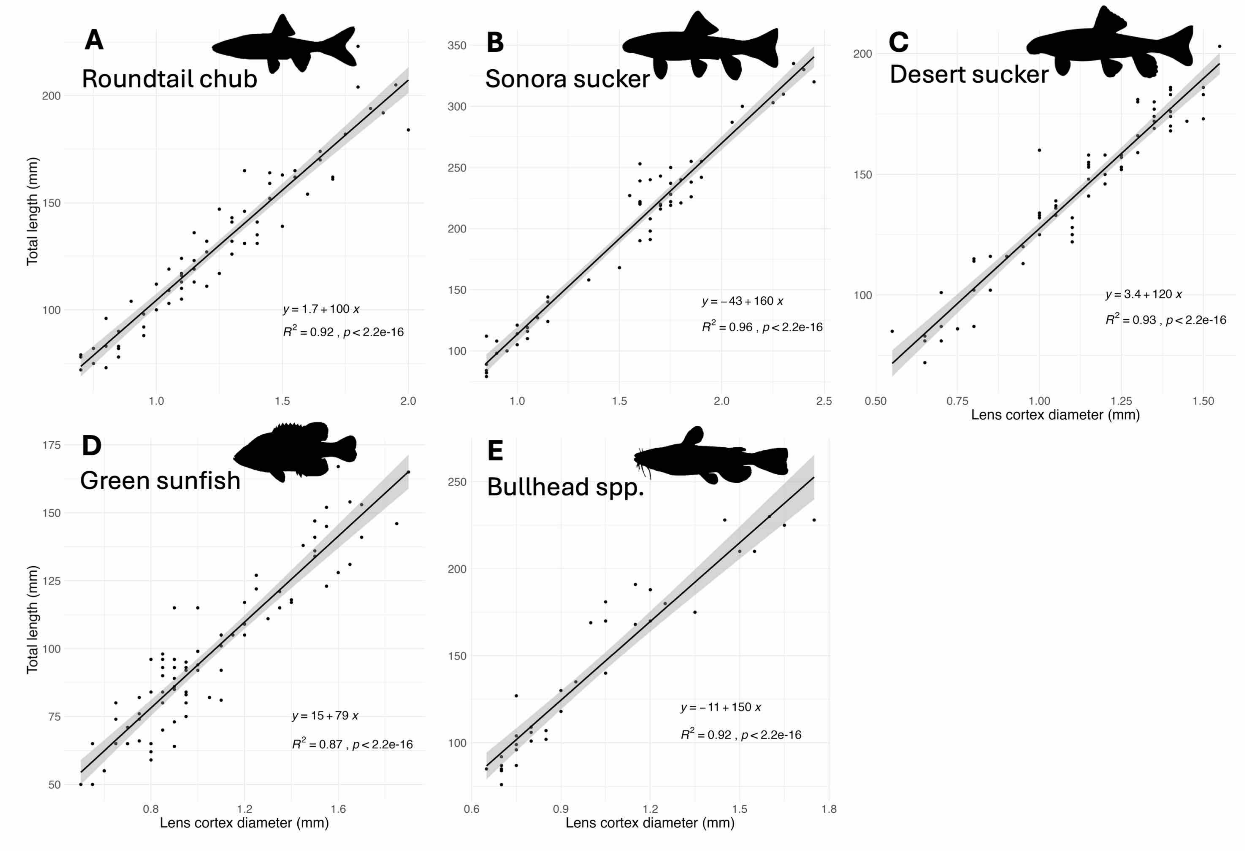

Figure A1.3: Total length vs. lens cortex diameter linear regression for roundtail chub (A), Sonora sucker (B), desert sucker (C), green sunfish (D), and bullhead spp. (E) in Burro Creek, Arizona.

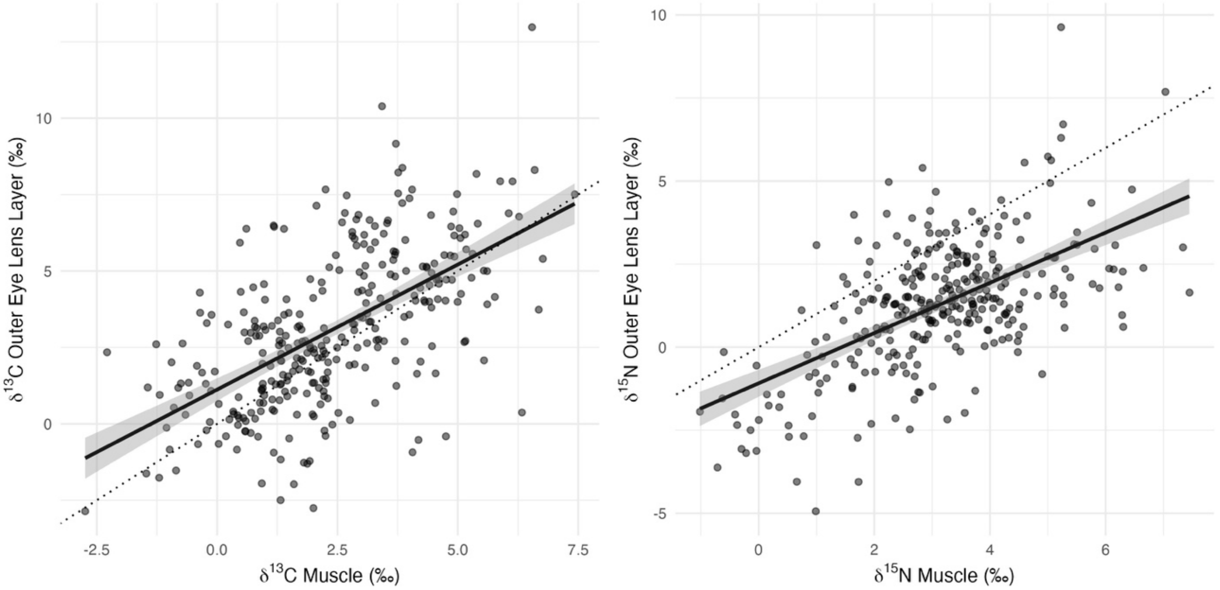

Figure A1.4: Muscle tissue compared to the outer eye lens layer for δ^{13}C (left) and δ^{15}N (right) for fish captured in Burro Creek, Arizona. Solid line created by linear regression model with grey band representing 95% confidence level for predictions from the linear model. Linear regression for δ^{13}C: slope = -0.42, intercept = 1.12, $p < 0.0001$, $R^2 = 0.33$ and δ^{15}N: slope = 0.47, intercept = 2.4, $p < 0.0001$, $R^2 = 0.39$. Fish without enough eye lens tissue to run more than one sample were excluded (so as not to compare muscle to the whole eye lens). Dotted line is 1:1 line. Units are per mil relative to Physidae snail spatial baseline.

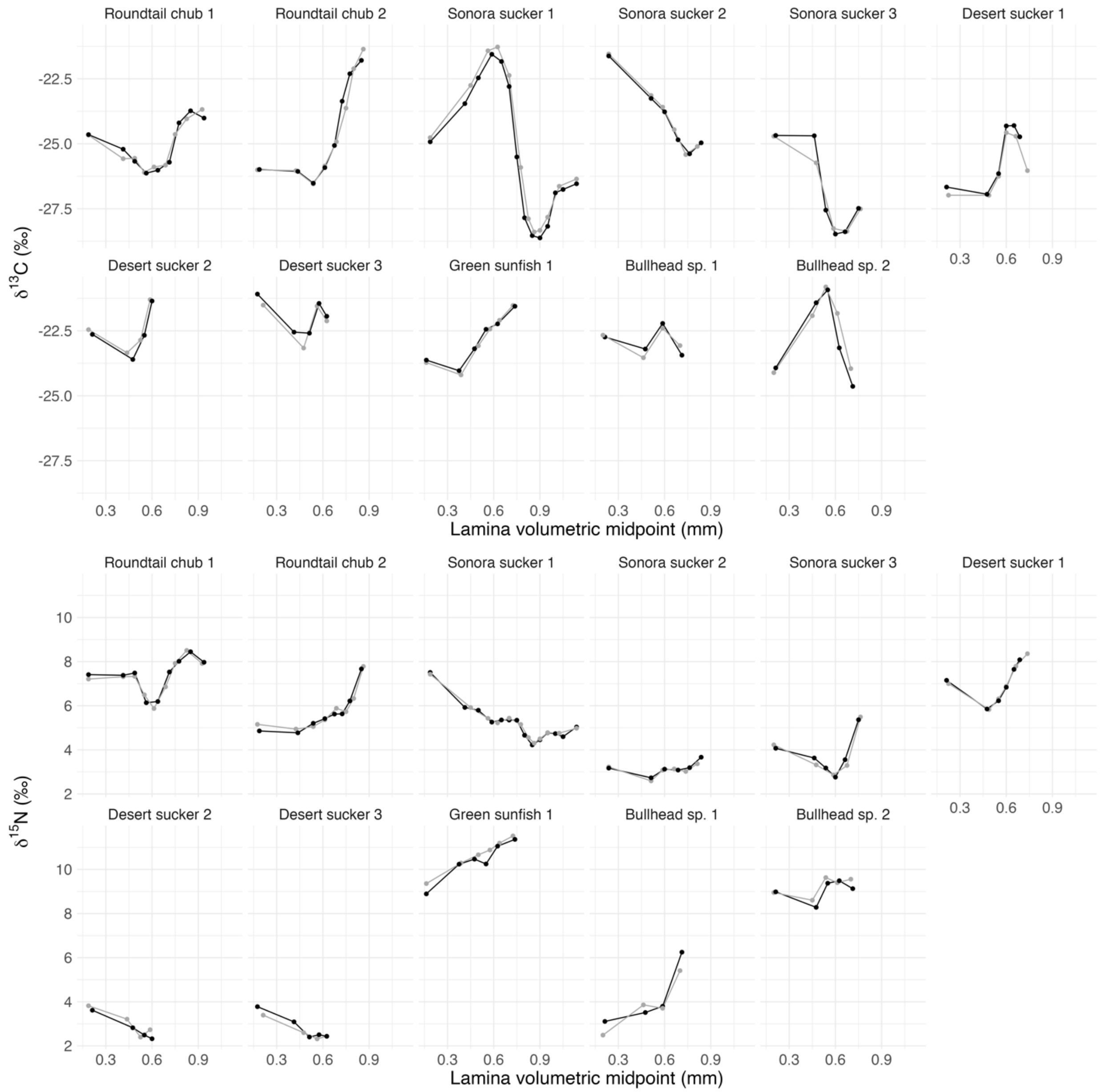

Figure A1.5: Stable isotope values $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) for right (grey lines) and left (black lines) fish eye lens layers from core to outer layer measured by the eye lens lamina volumetric midpoint of fish captured in Burro Creek, Arizona. There was no significant differences between left and right eye lenses (ANCOVA $P > 0.05$). Units are per mil relative to international standards (VPBD for $\delta^{13}C$ and air for $\delta^{15}N$).

Supplemental Methods: Age Back-calculation

The process of age at eye lens layer back-calculation was performed separately for each individual fish (Fig. A1.6). It began by plotting lens cortex diameter (mm) vs. total body length (mm; hereafter, fish length) for each species (Fig. A1.7), then performing quality control to remove outliers. Individual fish were removed from analysis at this stage based on visual inspection of the plot and notes taken during eye delamination. Next, species-specific fish length at each eye lens was estimated using bootstrapping of a linear regression model on the lens cortex diameter vs. total length relationship. For each fish, 1000 bootstrapping iterations were performed to calculate the linear equation used to estimate fish length at each eye lens layer (i.e., fish length estimate = eye layer volumetric midpoint * linear model slope + linear model intercept), resulting in 1000 fish length estimates at each eye lens layer.

Otolith radius at each eye lens layer was estimated using the linear relationship between otolith radius and fish length (Fig. A1.8), and the Fraser-Lee back-calculation method. Bootstrapping of the linear regression model of species-specific otolith radius (microns) vs. fish length (mm) relationship was performed for 1000 iterations for each fish, resulting in 1000 estimates of the “biological intercept” of otolith radius at length = 0. Next, an individual-specific growth line was fit between two anchor points on a plot of otolith radius (microns) vs. fish length (mm): the length-0 biological intercept and the length and otolith radius at capture (Fig. A1.9). For each of the 1000 estimates of fish length at each eye lens layer and each of the 1000 estimates of the biological intercept, this individual fish back-calculation growth line resulted in 1,000,000 estimates of otolith radius at each eye lens layer. We took the mean of these otolith radius estimates at each eye lens layer.

Age at each eye lens layer was estimated using a plot for each individual fish of the otolith radius (microns) vs. fish age (years) constructed from otolith annuli measurements, with an intercept at the origin (Fig. A1.10). Otolith radius estimates for each eye lens layer were plotted along the connected annuli points, assuming a linear growth relationship between annuli. The corresponding age values were then used to estimate age at each eye lens layer, with several corrections to follow. We subtracted 2 months (i.e., 2/12 years) from the estimated age of each eye lens layer because at the time of capture, the outer eye lens cortex was not representative of the current (April 2021) diet; it was formed 2-3 months prior. This corrects for the lag time that it takes tissue to reflect the diet of the consumer. An additional month (i.e., 1/12 years) was subtracted because we aged fish at whole integers (e.g., 1 year, 2 years), but at the time of capture, the fish had not yet reached a full year of age. Peak spawning is early May for all species, and we captured fish from April 1-14th. Individuals that were found to be outliers due to an imprecise delamination process resulting in strong over- or under-estimated eye lens layer ages were removed (ranging from 0-10 individuals per species).

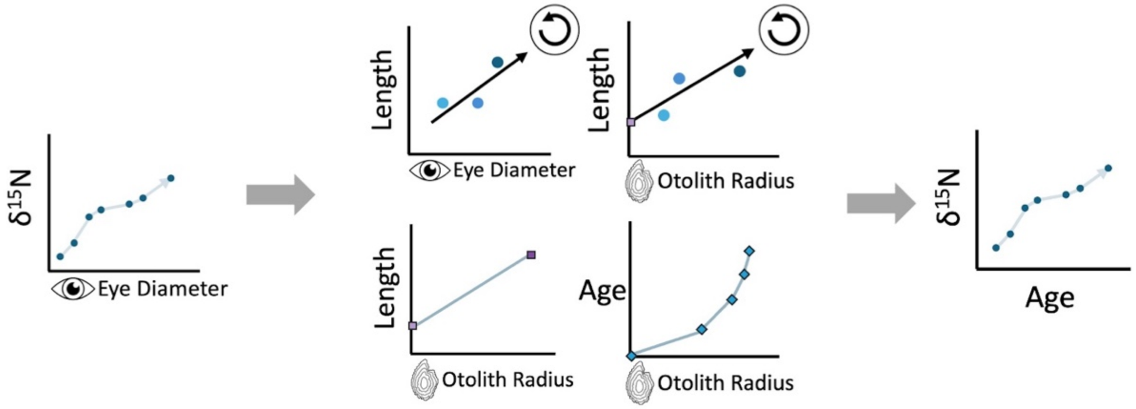

Figure A1.6: Conceptual diagram displaying fish age at eye lens layer back-calculation methods. The species-specific relationship between eye lens diameter and fish length is first used to estimate length at each eye lens layer. Next, the species-specific relationship between otolith radius and fish length is used to estimate the biological intercept (i.e., length at which otolith growth begins) used for the Fraser-Lee fish length back-calculation. This biological intercept (the light purple square on the y-axis) is then plotted for individual fish with their length and otolith radius at time of capture (dark purple square). This individual fish plot linking the otolith radius and fish length data points is used to estimate otolith radius at each eye lens layer. Finally, the individual fish relationship between otolith radius and age, assuming linear growth between otolith annuli, is used to estimate fish age at each eye lens layer. Bootstrapping is used to incorporate uncertainty in the species-specific relationships (circular arrows).

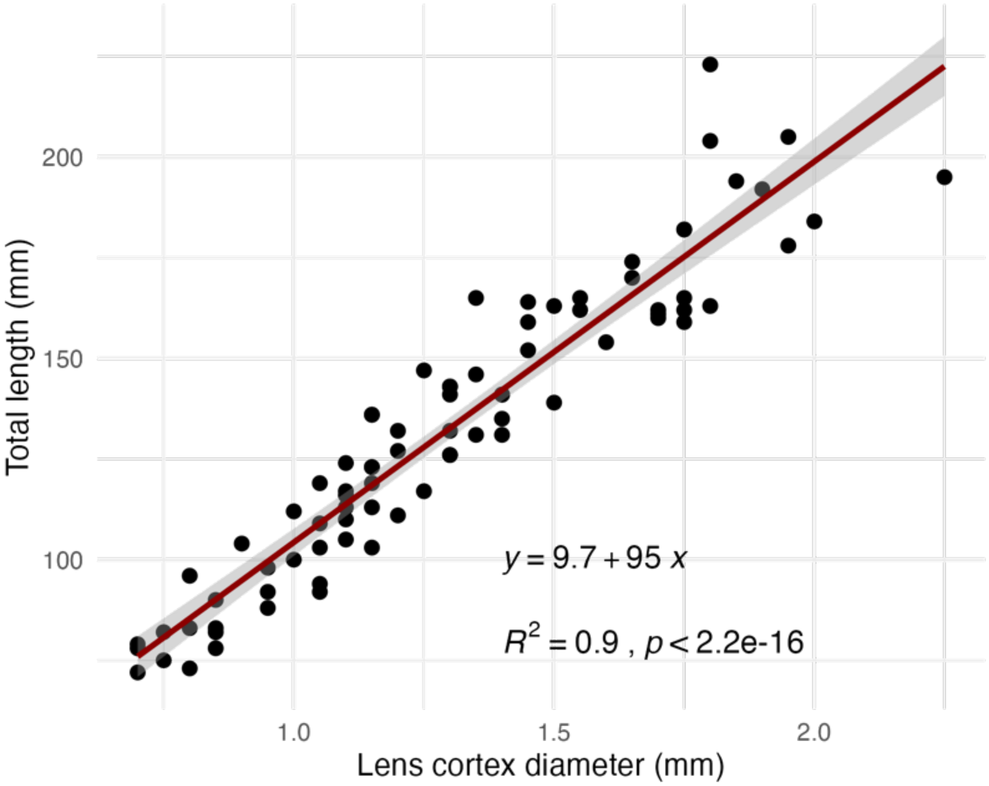

Figure A1.7: Linear regression of lens cortex diameter (mm) vs. fish total length (mm) of roundtail chub in Burro Creek, Arizona.

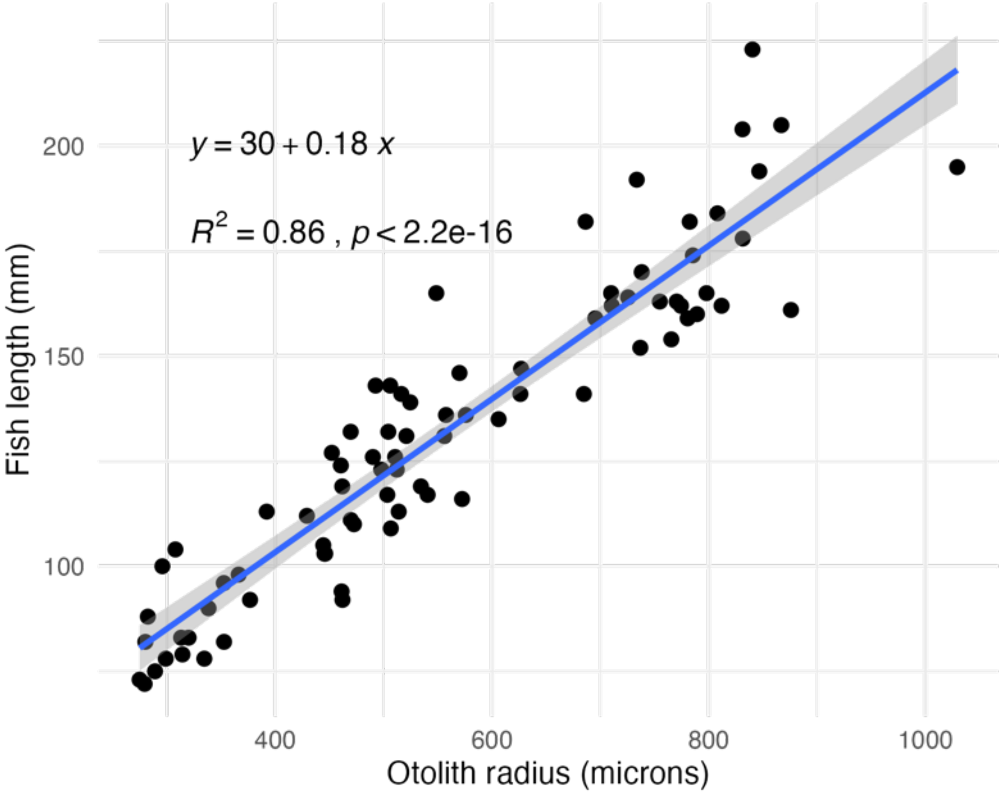

Figure A1.8: Linear regression of otolith radius (microns) vs. fish total length (mm) of roundtail chub in Burro Creek, Arizona.

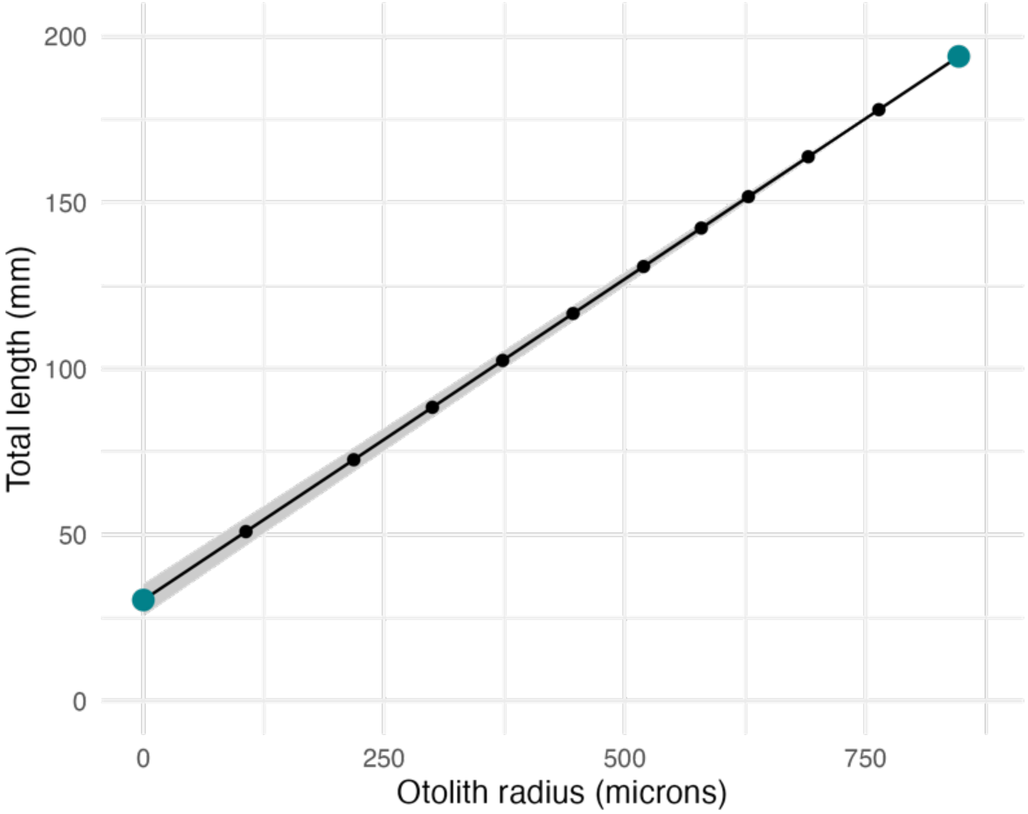

Figure A1.9: Otolith radius (microns) vs. total length (mm) for a single roundtail chub in Burro Creek, Arizona. The green points are the estimated biological intercept at length = 0 and the length and otolith radius of the individual fish at the time of capture. Black points represent eye lens layers plotted along the line based on their estimated total length at each eye lens layer, resulting in an estimate of the otolith radius at each eye lens layer. The grey ribbon shows the standard deviation of the 1000 biological intercept bootstrap samples, including uncertainty in the otolith radius estimates.

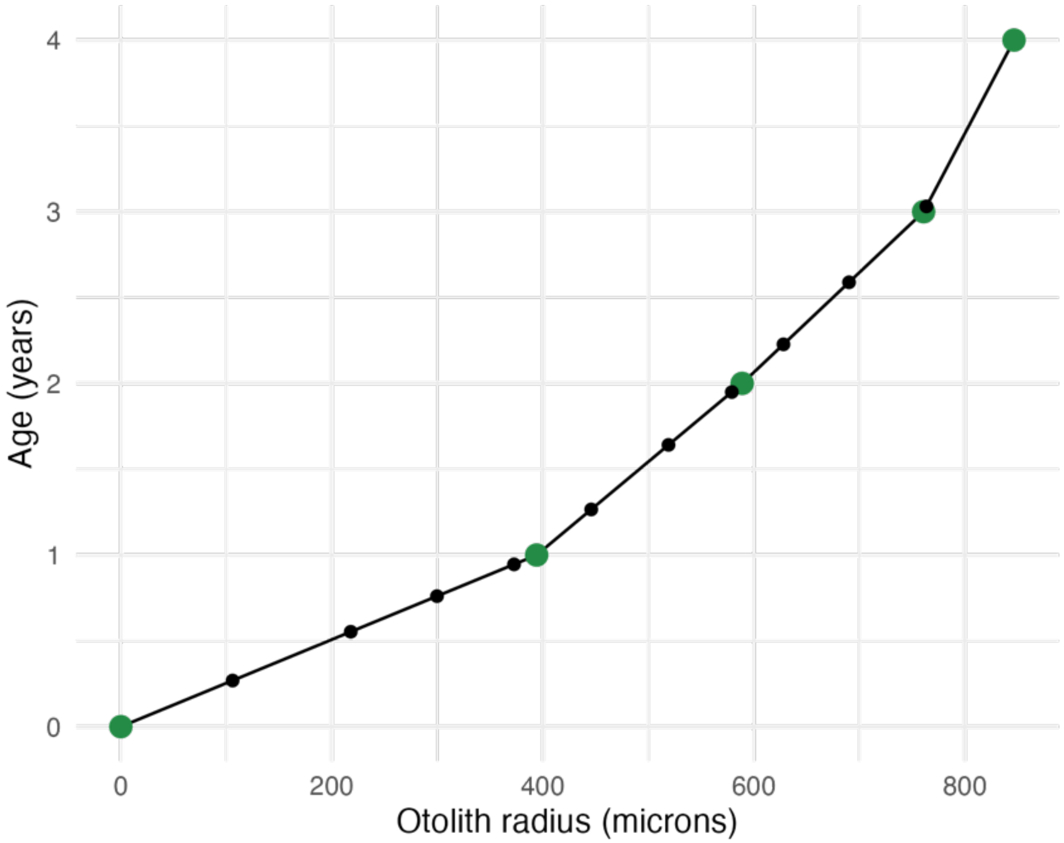

Figure A1.10: Otolith radius (microns) vs. age (years) for a single roundtail chub in Burro Creek, Arizona. Green points represent the otolith annuli measurements, assuming an intercept at the origin. Black points represent eye lens layers (mean otolith radius at each eye lens layer based on 1,000,000 bootstrap samples) used to calculate age.

Chapter 2. THE AGE OF RIVALRY: SHIFTING COMPETITIVE HIERARCHIES THROUGH ONTOGENY IN NATIVE AND INVASIVE STREAM FISHES

Publication history: This study was co-authored with Julian D. Olden. At the time that this dissertation was published, this chapter was in review for publication.

2.1 ABSTRACT

Competition for shared resources within and between species is a powerful force in community ecology. Modern coexistence theory predicts that higher intra-specific, relative to inter-specific, competition results in species coexistence because competitors are self-limiting. However, resource use is rarely constant across animal development; many species experience ontogenetic dietary shifts. Therefore, relative strengths of competition may change throughout ontogeny, leading to a reversal in competitive superiority between two species. Invasive species are often superior competitors due to their generalist feeding habits and high rates of resource exploitation. To quantify competition through ontogeny between invasive and native fishes, we measured isotopic niche overlap of individual lifetime trophic trajectories constructed using fish eye lens stable isotope analysis coupled with otolith growth measurements. We found that invasive green sunfish (*Lepomis cyanellus*) experienced higher intra-specific isotopic niche overlap through ontogeny relative to inter-specific overlap with three native fish species (*Gila robusta*, *Catostomus insignis*, *Catostomus clarkii*) in Burro Creek, Arizona. These native fish species experienced the highest isotopic niche overlap with green sunfish, known to be a superior competitor. The degree of competition experienced by native species increased through ontogeny, while invasive green sunfish were freed from high interspecific competition at older ages. Our results demonstrate that the coexistence in mixed native-nonnative communities is supported by modern coexistence theory. As invasive species continue to spread and proliferate, contemporary ecological communities are increasingly being managed for coexistence, rather than invader eradication. Understanding how relative competition transforms through ontogeny supports coexistence conservation in native-nonnative communities.

2.2 INTRODUCTION

In his seminal work *On the Origin of Species*, Charles Darwin posited that competition among organisms is a major force in the "struggle for existence" (Darwin 1859). Darwin's overarching hypothesis was that the fiercest competition is more likely to manifest between individuals of the same species, whereas competition is generally weaker between individuals from different coexisting species, as a function of their phylogenetic relatedness. Over a century later, it is now well recognized that species coexistence is influenced by a number of factors, including environmental conditions and species interactions that either promote or hinder species persistence (Chesson 2000). Competition for shared resources, in particular, is well recognized as a limiting mechanism in community ecology (MacArthur 1970, Tilman 1982).

Modern coexistence theory asserts that coexistence between two competitors is more likely when the strength of intra-specific competition among individuals of the same species exceeds interspecific competition among individuals of different species (Connell 1983, Chesson 2000, Barabás et al. 2018). The reason being is that high intra-specific competition is expected to be self-limiting and prevent the opposing species from being eliminated. Coexistence theory has been experimentally tested for a variety of taxa, including plants (Adler et al. 2018), invertebrates (Creese and Underwood 1982, Cross and Benke 2002), fish (Forrester et al. 2006, Zhang et al. 2024), and mammals (Sekijima and Sone 1994). However, field-based empirical investigations of species coexistence are historically rare (Armitage and Jones 2019) and limited by their temporal scope and ability to capture species interactions across developmental stages. Measuring the relative strength of intra- and inter-specific competition throughout ontogeny in nature continues to challenge ecologists.

Competitive interactions shift and transform throughout individual development due to changes in size, habitat use, and feeding habits. Ontogenetic dietary shifts are widespread among animals (Werner and Gilliam 1984, Nakazawa 2015) and may promote coexistence and community stability (Sánchez-Hernández et al. 2019, Anaya-Rojas et al. 2023), for example when the rank of competitive superiority between two species reverses during ontogeny (Connell 1983). Measuring competitive interactions across the continuum of age has thus far eluded researchers. Empirical studies have predominantly focused on competition across discrete stages (Louhi et al. 2014, Zhao et al. 2014, Cucherousset et al. 2020, Davis et al. 2025), while modeling approaches have integrated ontogenetic dietary shifts over continuous changes in body length (Bassar et al. 2017). Because dietary shifts are often continuous and do not necessarily scale linearly with body size, evaluating age-varying competition allows for a more robust assessment of resource competition across ontogeny.

The increasing threat of invasive species creates an opportunity to test coexistence theory, while concurrently incorporating increased knowledge of competitive interactions into management strategies. Competition is one of the major mechanisms through which invasive species contribute to native species imperilment (David et al. 2017), driven by the fact that these species are often superior competitors due to elevated rates of resource exploitation (Dick et al. 2017, Dominguez Almela et al. 2021) and high plasticity in feeding habits (Pettitt-Wade et al. 2015, Glassic et al. 2023). Coexistence between native and nonnative species has been attributed to higher intra-specific, relative to inter-specific, competition (Britton et al. 2018, Lewis et al. 2024), including among functionally analogous native and nonnative carp species in the Pearl River Basin, China (Zhang et al. 2024). Fundamental to understanding and predicting coexistence among species, both native and nonnative in origin, is the ability to estimate the relative strength of intra- and inter-specific resource competition among individuals throughout their entire lifespan.

Until now, empirical tests of modern coexistence theory incorporating ontogenetic dietary shifts have lagged behind theoretical claims due to limited methodological approaches. Combining stable isotope analysis and aging techniques of complementary structures holds promise for testing modern coexistence theory through ontogeny. Calculating the isotopic niche with carbon and nitrogen stable isotope analysis is frequently used to estimate a species' trophic niche (Layman et al. 2007, Jackson et al. 2011). While the assumptions inherent in representing the trophic niche with the isotopic niche are readily acknowledged (Bearhop et al. 2004, Newsome et al. 2007), strong isotope-diet relationships (Guzzo et al. 2013, Kingsbury et al. 2020, Shepta et al. 2023) support the use of isotopic niche overlap as a measure of trophic interaction strength and hence, competition. When applied to different tissues that record the chronology of feeding habits over time, ontogenetic shifts in competition can be measured. Such tissues include otter whiskers (Newsome et al. 2009), seal teeth (Riofrío-Lazo et al. 2012), shark vertebrae (Estrada et al. 2006), fish scales (Olden et al. 2019), cetacean skin (Wild et al. 2018), narwhal tusks (Dietz et al. 2021), turtle shells (Reich et al. 2007), and eye lenses of fish (Wallace et al. 2014), squid (Liu et al. 2020), birds (Hasegawa et al. 2025), and bears (Miura et al. 2025). The power of these tissues is amplified when combined with additional biological structures. For example, fish eye lens tissue is highly nitrogenous, but does not display clear time markers. When coupled with fish otoliths, which are commonly used to measure age and growth of fishes, but are low in nitrogen, these two structures can be used to time stamp stable isotope values throughout ontogeny. Although the idea of combining fish eye lenses and otoliths has been proposed (Tzadik et al. 2017), it has never before been achieved.

Using freshwater fish as a model system, we aim to quantify the relative competition strength within freshwater fish communities through ontogeny to evaluate coexistence between native and nonnative species. Many freshwater fishes undergo significant shifts in feeding habits as they age and grow in size (Sánchez-Hernández et al. 2019). We constructed lifetime trophic trajectories using an emerging method of combining fish eye lens tissue with otolith growth measurements. This novel approach creates individual stable isotope time series and allows for comparisons across populations and species. Stream communities of Burro Creek, AZ are dominated by native roundtail chub (*Gila robusta*), Sonora sucker (*Catostomus insignis*), desert sucker (*Catostomus clarkii*), and nonnative green sunfish (*Lepomis cyanellus*). Roundtail chub and green sunfish are omnivores that consume aquatic invertebrates early in life and become piscivorous through ontogeny, while Sonora suckers largely consume aquatic invertebrates, and desert suckers are primarily herbivorous, consuming mostly algae and detritus (Schreiber and Minckley 1981, Minckley and Marsh 2009).

Past studies of modern coexistence theory have typically focused on the coexistence of two species within the same trophic guild or similar phylogeny (Spaak and Schreiber 2023), but here we use stable isotope analysis to look past categorical guild classification and embrace the continuity of isotopic niches. Although representing distinct trophic guilds, these species' isotopic niches are expected to intersect and diverge throughout their lifespans due to ontogenetic dietary shifts. We hypothesize that competition will be asymmetrical between focal species and competitor pairs, with nonnative green sunfish impacted most by intra-specific competition, due to their superior competitive ability. Among the native fishes, we expect roundtail chub to experience the highest competition with green sunfish due to similarities in diet requirements that change with ontogeny. We generally hypothesize that intra- and inter-specific competition will be elevated among juvenile fishes (< 1 year of age), whose foraging is limited by body size and habitat use (Nunn et al. 2012). For both green sunfish and roundtail chub, competition with the two sucker species is expected to be highest early in ontogeny before sunfish and chub shift to piscivory.

2.3 METHODS

Fish sampling: Fish were collected from mixed native-nonnative communities of the Burro Creek basin, AZ between April 1-12th, 2021 using electrofishing and occasional seining. Sampling occurred in a 100-m stretch of stream containing representative riffle-run-pool habitats in each of twelve sites. One-pass electrofishing was employed using a Smith Root 24 Backpack Electrofishing Unit with a standard anode (25 cm diameter ring attached to a 2m pole) and cathode (3.2m wire cable) following standard protocols (Bonar et al. 2009). The most common fish species encountered are green sunfish, roundtail chub, Sonora sucker, and desert sucker (Appendix 2: Table A2.1). In addition to fishes, benthic macroinvertebrates were collected within each site to establish the stable isotope baseline across sites. Ten of the most common taxa (out of 35 collected) were processed for stable isotope analysis, representing collector/filterer, collector/gatherer, scraper, and predator functional feeding groups.

Stable isotope analysis: We processed fish eye lens tissue for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis (SIA) to determine individual and species-level isotopic niches through ontogeny (Fig. 2.1; Wallace et al. 2014, Quaeck-Davies et al. 2018). The dissection or delamination, of spherical fish eye lens tissue was performed using a light microscope with an ocular micrometer and high precision forceps (Appendix 2: Fig. A2.1a). Lens diameter was measured between each delamination to calculate each layer's volumetric midpoint.

Samples processed for SIA included fish eye lens tissue and macroinvertebrates. Approximately 0.5 mg samples were dried in an oven at 55° C for 24-48 hours, then crushed, homogenized, and packed into tin capsules. We used an Elemental Analyzer (NA 2500; CE Instruments, Wigan, United Kingdom) interfaced with a Delta V Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts) at the University of Washington. Stable isotope ratio data are reported in permil (‰) units as the delta (δ), or relative difference, from a standard per the following equation: $\delta X = ((R_{sample}/R_{standard}) - 1) * 1000$ where X represents ^{13}C or ^{15}N and R represents the ratio of heavy to light isotope for each element (i.e.,

${}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$). Fish tissue samples were referenced to Physidae snails collected at each site as an isotopic baseline (Appendix 2: Table A2.2) to allow for comparisons between sites due to their relatively slow turnover rate (Post 2002, Jardine et al. 2014). Baseline changes over time were expected to be minimal due to the short length of time included in our eye lens time series (< 6 years). This is also supported by previously collected macroinvertebrate stable isotope data in the same sites from 2016 (Rogosch and Olden 2020), with high overlap and no consistent trend between years for three taxa (Appendix 2: Fig. A2.2). Food web structure based on stable isotope analysis showed overall differentiation in $\delta^{13}C$ and $\delta^{15}N$ separating the various prey items: filamentous algae, coarse particulate organic matter, benthic macroinvertebrates, and fishes (Appendix 2: Fig. A2.3). The prey categories differ in ${}^{13}C/{}^{12}C$ and ${}^{15}N/{}^{14}N$ with a total range of 8.72‰ and 5.51‰, respectively.

Fish aging: Otoliths were extracted from all fish for aging analysis, then mounted using Crystalbond onto a microscope slide and polished to expose nuclei and edge increments (following Chittaro et al. 2020). Lapillar otoliths were used to age native fishes (Appendix 2: Fig. A2.1b) and sagittal otoliths were used to age green sunfish. Both authors (readers) independently aged the otoliths (with no other information provided), and age estimates were compared and evaluated via percent agreement and among-reader precision (Quist et al. 2007). First-time age estimates resulted in 86% agreement between readers across all species, with 76% of disagreements within 1 year. Among-reader precision was 4.8, calculated as the coefficient of variation (CV) averaged across individual fish. We measured distance from the core to each otolith annulus using ImageJ along a consistent radius line for each species (Schneider et al. 2012).

Statistical analysis: We constructed lifetime trophic trajectories of individual fish using fish eye lens $\delta^{13}C$ and $\delta^{15}N$ values in isotopic niche space. These trophic trajectories were converted to time series in combination with otolith growth measurements, then smoothed using cubic spline interpolation. Isotopic niche overlap between and within species was calculated across ontogeny to create competitive interaction surface heatmaps (approach illustrated in Fig. 2.2 with age back-calculation described in detail in Appendix S2 of Diallo and Olden 2025). Pairwise competitor comparisons distinguish between the species subject to competition and the species exerting competition, hereafter referred to as the “focal species” and “competitor species,” respectively.

Age at each eye lens layer was calculated from linear regression models of eye lens diameter and otolith radius vs. fish length, coupled with otolith annuli measurements for each individual fish (Fig. 2.2: step 2). Fish length at the volumetric midpoint of each eye lens layer was first estimated using the linear model predicting total length from lens diameter for each species with bootstrapping (1000 iterations) to account for uncertainty in estimates. The strong relationship between eye lens diameter and total length has been documented for many fish species (Tzadik et al. 2017, Quaeck-Davies et al. 2018), including this study (Appendix 2: Fig. A2.4). Next, the otolith radius at each eye lens layer was estimated from individual linear models of the Fraser-Lee biological intercept (otolith radius at length 0) and measurements at time of capture for each fish, with bootstrapping (1000 iterations) of the biological intercept based on the otolith radius vs. fish length linear models. Length-at-age back-calculation methods (Quist et al. 2012) were used to estimate age at each eye lens layer from otolith annuli growth measurements for each individual. Throughout the age back-calculation process, uncertainty was propagated using bootstrapping of linear regression models and performing subsequent steps on each estimate until the final mean age was calculated (i.e., the mean of 1,000,000 age estimates for each eye lens layer). A smoothing of individual trophic trajectories was performed using natural cubic spline interpolation (Fig. 2.2: step 3) and $\delta^{13}C$ and $\delta^{15}N$ values were selected at monthly intervals from each individual time series to facilitate direct comparison across individuals and species.

The magnitude of intra- and inter-specific competition was inferred as the degree of isotopic niche overlap between individuals when found in sympatry. For co-occurring individuals, isotopic niche overlap was measured for each month of an individual’s life in relation to the centroid of the isotopic niches defined by all individuals of the same (intra-specific) or different (interspecific) species grouped according to monthly age (Fig. 2.2: step 4) then expanded across ontogeny for the focal species and each competitor (Fig. 2.2: step 5). We maintained sample sizes at ≥ 5 individuals and isotopic niches were calculated as standard ellipses with a correction for small sample sizes (Jackson et al. 2011). Overlap between an individual focal species isotopic position and the centroid of the competitor’s isotopic niche at each interval was measured using the squared Mahalanobis distance, D^2, the distance between two points in multivariate space (i.e., not Euclidian distance). The squared Mahalanobis distance is calculated as $D^2 = (x - \mu)' * C^{-1} *$

(x - μ) where x is a vector representing the individual isotopic position, μ is the mean vector of the competitor's isotopic distribution, or the niche centroid, and C is the covariance matrix of the competitor's isotopic distribution, all in $\delta^{13}C$ - $\delta^{15}N$ isotopic space. A demonstration of isotopic niche overlap, measured using squared Mahalanobis distance in C-N biplot space, is provided in the Appendix (Appendix 2: Fig. A2.5). Points were classified as significantly overlapping in isotopic niche based on a chi-square distribution. Hereafter, the isotopic distance is used to refer to the squared Mahalanobis distance. Mean isotopic distance and proportion of individuals with significant overlap was calculated at each monthly time step for each focal species – competitor pair, then visualized as competitive interaction surface heatmaps. Though not all age combinations are equally likely (e.g., a 1-year-old and a 6-month-old green sunfish), protracted spawning seasons led us to presume that most of the competitive interaction space is possible. To summarize intra- and inter-specific competitive interactions over the focal species' lifetimes, we averaged isotopic distance across the range of competitor species' ages. Rates of change in competition through ontogeny were measured by modeling time series as biased random walks for each focal species – competitor pair using the MARSS package (Holmes et al. 2024). The biased random walk was estimated as $D^2_t = D^2_{t-1} + u + w_t,\ w_t \sim \mathrm{N}(0, q)$ where D^2_t and D^2_{t-1} are the mean squared Mahalanobis distances at age t and $t-1$, respectively. The variable u is the drift term representing the rate of change, and w_t is the error term with variance q. All analyses were performed with R version 4.4.0 (R Core Team 2024).

2.4 RESULTS

The ontogenetic timeline of isotopic niche overlap among fishes revealed evidence for varying degrees of intra- vs. inter-specific competition between native and nonnative species. Green sunfish exhibited high intra-specific isotopic niche overlap (low isotopic distance) across their entire ontogeny, especially for young-of-the-year (YOY) individuals (Fig. 2.3A). Isotopic niche overlap between green sunfish and roundtail chub was most prevalent during the first two years of chub life, with YOY green sunfish demonstrating the greatest overlap (Fig. 2.3B). This band of supposed inter-specific competition narrowed through green sunfish ontogeny, resulting in relatively low isotopic niche overlap between the species for green sunfish greater than 1 year of age. Green sunfish isotopic niche overlap with Sonora sucker was relatively high for YOY green sunfish and Sonora sucker less than 2 years of age, but decreased through green sunfish ontogeny (Fig. 2.3C). Isotopic niche overlap between green sunfish and desert sucker was remarkably consistent regardless of desert sucker age, starting high early in green sunfish ontogeny, then steadily decreasing through time (Fig. 2.3D).

Roundtail chub competitive interaction surfaces show clear differences between competitor species. Roundtail chub intra-specific isotopic niche overlap was relatively constant across developmental stages, though most pronounced after 2 years of age (Fig. 2.3E). The strongest isotopic niche overlap roundtail chub experienced through ontogeny was with green sunfish (Fig. 2.3F). Up to 2 years of age, roundtail chub isotopic niche overlap was highest with green sunfish aged 0.6-1.25 years. This stretch of high isotopic niche overlap and inferred competition expanded to include all ages of green sunfish for roundtail chub older than 2 years. Roundtail chub isotopic niche overlap with Sonora sucker was greatest for Sonora suckers less than 2 years, with a stark decrease in isotopic niche overlap for older Sonora suckers (Fig. 2.3G). However, isotopic niche overlap increased between the oldest roundtail chub (> 3 years) and Sonora sucker. Isotopic niche overlap between roundtail chub and desert sucker was relatively high with desert suckers from 1-1.5 years, regardless of roundtail chub age, and decreased with desert sucker age over 1.5 years (Fig. 2.3H). Sonora and desert sucker competitive interaction surfaces are provided in the Appendix (Appendix 2: Fig. A2.6). Isotopic niche overlap at the oldest ages was frequently measured with lower sample sizes between 5-10 individuals (e.g., roundtail chub and Sonora sucker; Fig. 2.3G).

Competitive interactions, estimated according to squared Mahalanobis distances in isotopic space averaged over the range of competitors ages, were found to fade in and out through ontogeny. Green sunfish demonstrated the greatest isotopic niche overlap with conspecifics, suggesting high intra-specific competition for resources across the entire green sunfish lifespan (Fig. 2.4A). With age, the level of isotopic niche overlap between green sunfish and interspecific competitors decreased steadily, with this gap between the relative strength of intra- vs. inter-specific isotopic niche overlap widening quickly after 0.5 years of age. Across the developmental timeline, roundtail chub demonstrated the consistently highest isotopic niche overlap with green sunfish, followed by conspecifics and desert sucker (Fig. 2.4B). Notably, roundtail chub transitioned from weak to strong isotopic niche overlap with Sonora sucker with age (Fig. 2.4B); the large variability in overlap stemming from varying degrees of inter-specific competition associated with different life stages of Sonora sucker (Fig. 2.3G). Highest isotopic niche overlap for Sonora sucker were with green sunfish and desert sucker, and the lowest with roundtail chub and conspecifics, particularly at younger ages of Sonora sucker (Fig. 2.4C). The degree of isotopic niche overlap with Sonora sucker depended on the age of inter-specific competitors (Fig. 2.3C, G). Similarly, desert sucker experienced the greatest isotopic niche overlap with green sunfish, followed by roundtail chub, conspecifics, and Sonora sucker (Fig. 2.4D).

Lifetime trends in isotopic niche overlap through ontogeny show a clear distinction between the native and nonnative species (Fig. 2.5). Aging nonnative green sunfish experienced decreasing isotopic niche overlap with each of the native species, as well as conspecifics, represented by the negative rates of change estimated through modeling the time series as biased random walks. By contrast, native species primarily experience increasing or relatively low overall change in isotopic niche overlap through ontogeny.

2.5 DISCUSSION

By combining fish eye lens stable isotope analysis with otolith aging techniques, we offer novel insight into the dynamics of intra- and inter-specific competitive interactions through ontogeny. Our findings provide strong evidence that coexistence between native and nonnative fishes is supported by competition theory. As predicted, nonnative green sunfish intra-specific competition, inferred by high isotopic niche overlap, exceeded levels of inter-specific competition through ontogeny, whereas for all native species, inter-specific competition with green sunfish was consistently higher than intra-specific competition with conspecifics. This evidence for asymmetric competition reflects the superior competitive ability of green sunfish relative to the native species (Werner and Hall 1977, Lemly 1985, Moran et al. 2018), but diminishes the likelihood of competitive exclusion because of self-limitation of green sunfish populations through intra-specific competition (Chesson 2000). Support for higher intra-, relative to inter-, specific competition resulting in coexistence has been documented between other native and nonnative fish species, in experimental (Anaya-Rojas et al. 2021, Lewis et al. 2024) and field settings (Zhang et al. 2024). A mechanism for reduced intra- or inter-specific competition may be niche divergence, documented with native and nonnative fishes (Britton et al. 2018, Czeglédi et al. 2024), skates (Simpson et al. 2019), and cephalopods (Golikov et al. 2020).

Modern coexistence theory was initially described between a single life stage of two species at a single point in time (Connell 1983, Chesson 2000). However, there is growing recognition that the intensity of competition can change throughout ontogeny, both within and between species (Sánchez-Hernández et al. 2019). This study provides stable isotope evidence of ontogenetic dietary shifts over the lifetime of individuals where competitors fade in and out through species development. Nonnative green sunfish faced the highest inter-specific competition early in ontogeny, which quickly weakened with age as their diet changed, demonstrating increasing isotopic niche separation from their native species competitors. By contrast, roundtail chub matured into greater resource competition with green sunfish, including greater isotopic niche overlap with a wider range of green sunfish ages, making them increasingly vulnerable to competitive impacts. Increased competition at specific developmental stages may lead to reduced growth (Baxter et al. 2007, Houde et al. 2015, Britton et al. 2018), with impacts to survival and recruitment (Olson 1996, Post 2003). Competition as measured by isotopic niche overlap has been documented between native and invasive fishes at discrete age classes (Cucherousset et al. 2020) and size categories (Czeglédi et al. 2024). Previous modeling efforts predicted that coexistence is more likely if one competitor shifts its niche with growing body size while the other does not (Bassar et al. 2017). Here, our results reveal subtle shifts in isotopic niche through ontogeny and illustrate the importance of measuring continuous ontogenetic dietary shifts to capture potential bottlenecks where competition is most acute.

The interplay of competition and predation manifests with intraguild predation. In addition to competition, coexistence is influenced by intraguild predation, in which a predator consumes smaller individuals of a competitor. Widespread among omnivorous species, intraguild predation reduces potential exploitative competition (Polis et al. 1989, Arim and Marquet 2004). Both green sunfish and roundtail chub likely engage in intraguild predation due to their omnivorous diets, including predation on small fish as adults (Minckley and Marsh 2009). Ecological theory predicts that intraguild predation destabilizes species coexistence unless the intraguild prey is a superior competitor and resources are limited (Holt and Polis 1997, Morin 1999); a scenario with limited empirical evidence (Tuckett et al. 2021). Both green sunfish and roundtail chub are piscivores as adults (Dudley and Matter 2000, Quist et al. 2006), but stable isotope analysis within our system is unable to distinguish between general piscivory and intraguild predation. Roundtail chub intraguild predation may contribute to coexistence with the superior competitor green sunfish, or intraguild predation by green sunfish may further imperil the native roundtail chub, making long-term coexistence less likely (Henkanaththegedara and Stockwell 2014, Goldberg et al. 2022). The magnitude of intraguild predation among freshwater fishes remains an important, but largely unstudied, phenomenon.

Our methods expand the study of competitive interactions using isotopic niche overlap by applying an additional dimension of time with the use of fish eye lens tissue. The use of fish eye lenses in ecology remains nascent, expanding only in recent years to quantify individual trophic niche and habitat use (Faletti and Stallings 2021, Young et al. 2022, Bastos et al. 2024). Previous studies have alluded to changing competition intensity due to high intra-specific variability and changes in niche overlap (Simpson et al. 2019, Curtis et al. 2020), but have been limited in their inter-individual comparisons by the units (eye lens diameter) measured and assigned to stable isotope values. Others have taken the estimates a step further, by predicting fish length at each eye lens layer value (Young et al. 2022, Bastos et al. 2024). Here, we leveraged well-established relationships between fish length and eye lens diameter, as well as fish length and otolith radius relationships, to be able to estimate fish age for specific eye lens layers. This has the benefit of allowing comparison of geographically distinct populations and species, with different growth rates, on the same scale of fish age. Future research can also incorporate biotic and abiotic changes over time (e.g., management actions or seasonal climate conditions). Applying SIA to additional incrementally grown biological structures for lifetime trophic ecology is possible for a wide variety of taxa using hair, bones, and teeth (Estrada et al. 2006, Knoff et al. 2008, Newsome et al. 2009, Pablo-Rodríguez et al. 2016). If the growth rates of those tissues are known, the SIA values can be assigned a time stamp (Stern 2024). Fish eye lenses grow in discrete sections every 2-3 months, though uncertainty remains about this deposition rate (Wallace et al. 2014, Granneman 2018), requiring additional measures of individual growth to estimate fish age at specific eye lens layers. Therefore, combining otolith aging structures with fish eye lenses is a robust method for creating SIA time series to study ontogenetic dietary shifts on a finer time scale.

The isotopic niche is a widely used metric for quantifying the trophic niche (Layman et al. 2007, Marshall et al. 2019) despite a number of implicit assumptions (Bearhop et al. 2004, Newsome et al. 2007). Following isotopic niche estimation, resource competition may be approximated via niche overlap (Ogloff et al. 2019, Larocque et al. 2021). This has been evidenced by field studies evaluating dietary overlap from stomach contents in concert with $\delta^{13}C$ and $\delta^{15}N$ isotopic niche overlap (Guzzo et al. 2013, Kingsbury et al. 2020, Shepta et al. 2023). Overlapping isotopic niches may not represent resource competition if resource use is segregated in time or space, distinct prey taxa produce indistinct stable isotope values, or resources are not limited. Within our study system, fishes overlap in their resource use in space due to the small stream size and in time based on their visual foraging methods. The $\delta^{13}C$ - $\delta^{15}N$ prey space contains 4 distinct prey categories, filamentous algae, coarse particulate organic matter, benthic macroinvertebrates, and fishes, which the fish species studied herein feed upon throughout ontogeny. The sufficient distance between prey categories in $\delta^{13}C$ - $\delta^{15}N$ space allows for discrimination between them, leading us to conclude that niche overlap represents putative competition. Consumer stable isotopes may fluctuate across time or space due to variable basal resource stable isotope values. To correct for a spatially variable stable isotope baseline, we referenced the fish eye lens stable isotope data to a relatively long-lived macroinvertebrate found at all sites, Physidae snails. Analyzing isotopic niche overlap based on estimated fish age, rather than estimated date, assumes no significant changes in the stable isotope baseline or prey availability through time. A temporal baseline correction was deemed unnecessary due to high overlap and variability in stable isotope values of macroinvertebrates collected in 2016 and 2021.

This research advances our fundamental understanding of species coexistence as it relates to competition within and between species. Ecological communities are dynamic and composed of multiple interacting species, with individuals exhibiting ontogenetic dietary shifts. Modern coexistence theory was initially described between two competing species, challenging the extension of predictions to ecological communities with multiple interacting species. However, analytical advances are showing support for extending pairwise interaction rules to multi-species communities, including higher-order interactive effects (Gibbs et al. 2022). Ecological communities inhabited by multiple invasive species are increasingly common due to growing rates of spread (Lockwood et al. 2013), with potential for interactions that dampen or amplify their effects on native communities (Green et al. 2011, Jackson 2015). Competition networks have been developed to quantify intra- and inter-specific competition among multiple species (Pelage et al. 2022, Koutsidi et al. 2024) to better understand community stability, with applications for the study of biological invasions (Godoy 2019). Our study provides another dimension for future research, paving the way for dynamic competition networks that reflect fluctuations in competition due to ontogenetic dietary shifts.

Capturing the dynamics of intra- and inter-specific resource competition through ontogeny leads to a more complete understanding of community coexistence. This is increasingly relevant in contemporary communities consisting of native and nonnative species. As invasive species continue to spread and negatively impact native communities, control efforts are increasingly deployed to suppress or eradicate populations (Rytwinski et al. 2019). Knowing how the intensity of competitive impacts changes throughout the lifespan of an imperiled species, we can better manage invasive competitors to reduce those impacts. Unforeseen ecological outcomes in response to invasive control efforts can also be avoided if we better understand species interactions. Due to the proliferation of nonnative species, coexistence conservation has become a new standard in natural resource management (Evans et al. 2022). Understanding lifetime competitive interactions will support management for coexistence, a paramount objective for novel assemblages within an increasingly invaded world.

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2.8 FIGURES

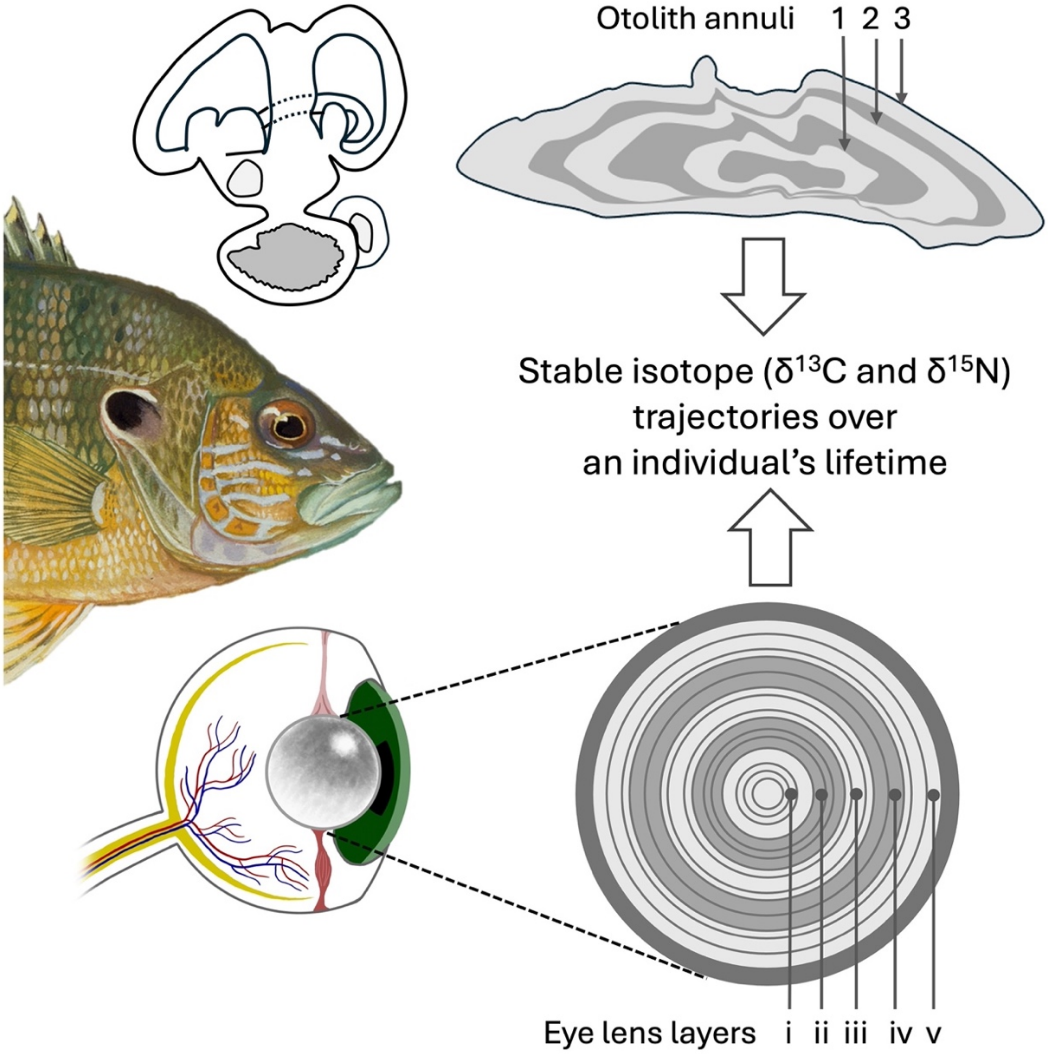

Figure 2.1: Diagram of green sunfish otolith (top) and eye lens (bottom) in terms of their biological structures (left) and cross-sections (right). Otolith annuli are labeled 1-3 for each year of fish age and growth. Eye lens layers are labeled from the core (i) representing early ontogeny to the outer layer (v) representing activity prior to capture. When processed for δ^{13}C and δ^{15}N stable isotope analysis, the sequence of eye lens layers provide a lifetime trophic trajectory of an individual fish. This is combined with otolith aging measurements to link stable isotope values to fish age. Fish illustration by Duane Raver (Public domain, U.S. Fish and Wildlife Service National Digital Library). All other illustrations by Jessica Diallo.

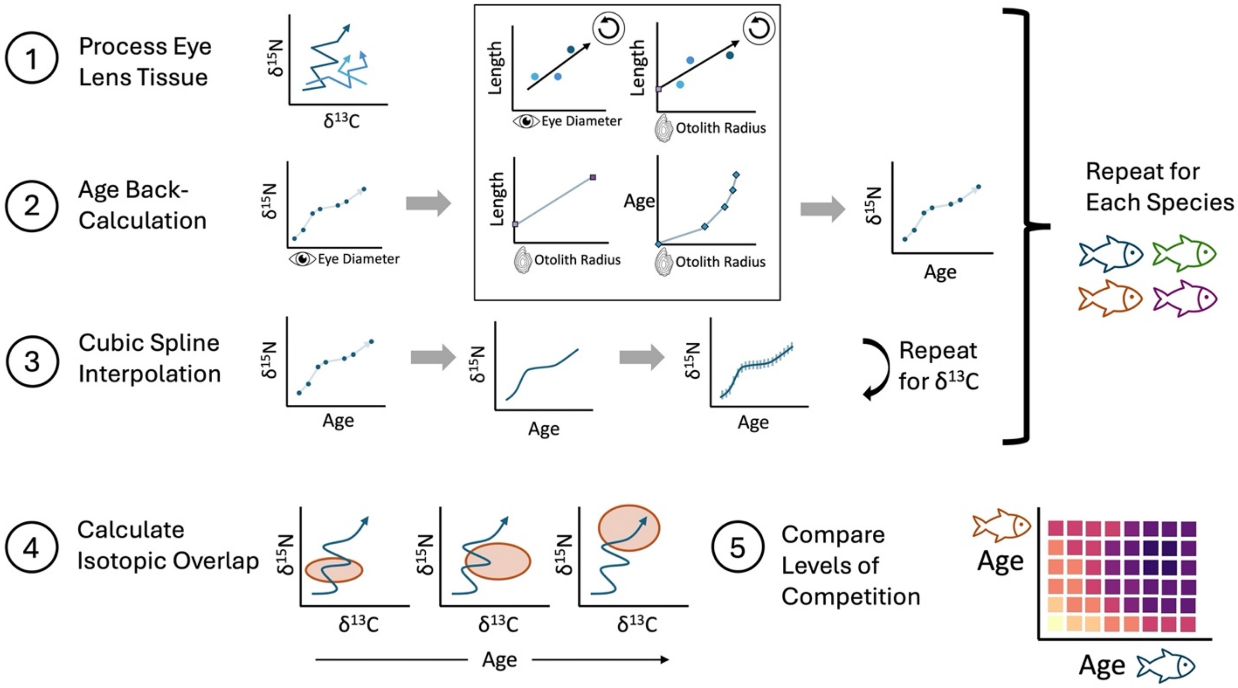

Figure 2.2: Conceptual diagram displaying methods used to calculate isotopic niche overlap as a measure of competition potential between focal species and competitors (green sunfish, roundtail chub, Sonora sucker, and desert sucker). After eye lens tissue is processed for stable isotope analysis (step 1), fish age at each eye lens layer is back-calculated (step 2). This step uses the species-specific relationship between eye lens diameter and fish length to estimate length at each eye lens layer. Next, the species-specific relationship between otolith radius and fish length is used to estimate the biological intercept (i.e., length at which otolith growth begins) used for the Fraser-Lee fish length back-calculation. This biological intercept (the light purple square on the y-axis) is then plotted for individual fish with their length and otolith radius at time of capture (dark purple square). This individual fish plot linking the otolith radius and fish length data points is used to estimate otolith radius at each eye lens layer. Finally, the individual fish relationship between otolith radius and age, assuming linear growth between otolith annuli, is used to estimate fish age at each eye lens layer. Bootstrapping is used to incorporate uncertainty in the species-specific relationships (circular arrows). Step 3 is cubic spline interpolation to smooth out the trophic trajectories and select monthly age increments. Step 4 is the measure of isotopic distance (squared Mahalanobis distance) between competitor species isotopic niches at monthly increments (orange

ellipses) and focal species individuals at monthly increments (blue line). Step 5 is taking the mean isotopic distance measured at each monthly increment for the focal species individuals to create competitive interaction surfaces of the focal species (blue fish, x-axis) in relation to the competitor species (orange fish, y-axis).

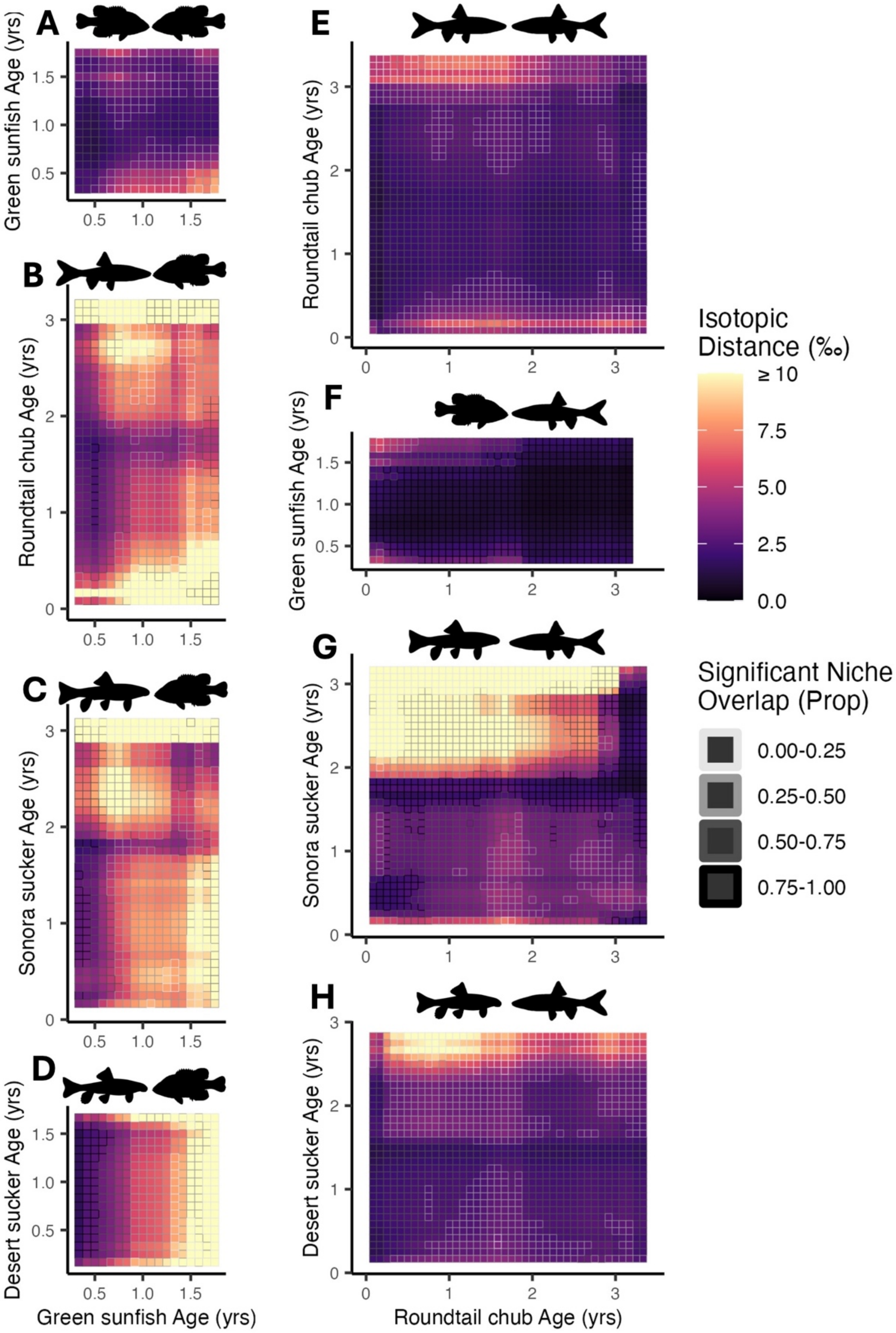

Figure 2.3: Competitive interaction surface displaying isotopic distance across the lifetimes of focal species green sunfish (plots A-D) and roundtail chub (plots E-H) with

competitors. Isotopic distance is defined as the squared Mahalanobis distance (D^2), which measures the distance from an individual point to the centroid of the competitor's isotopic niche in C-N biplot space. Interaction squares represent a month of time and are outlined a shade of grey representing significant niche overlap, or the proportion of the focal species individuals that significantly overlap with the competitor's isotopic niche based on a chi-square distribution. Fish silhouettes display the competitor on the left, focal species on the right (not to scale).

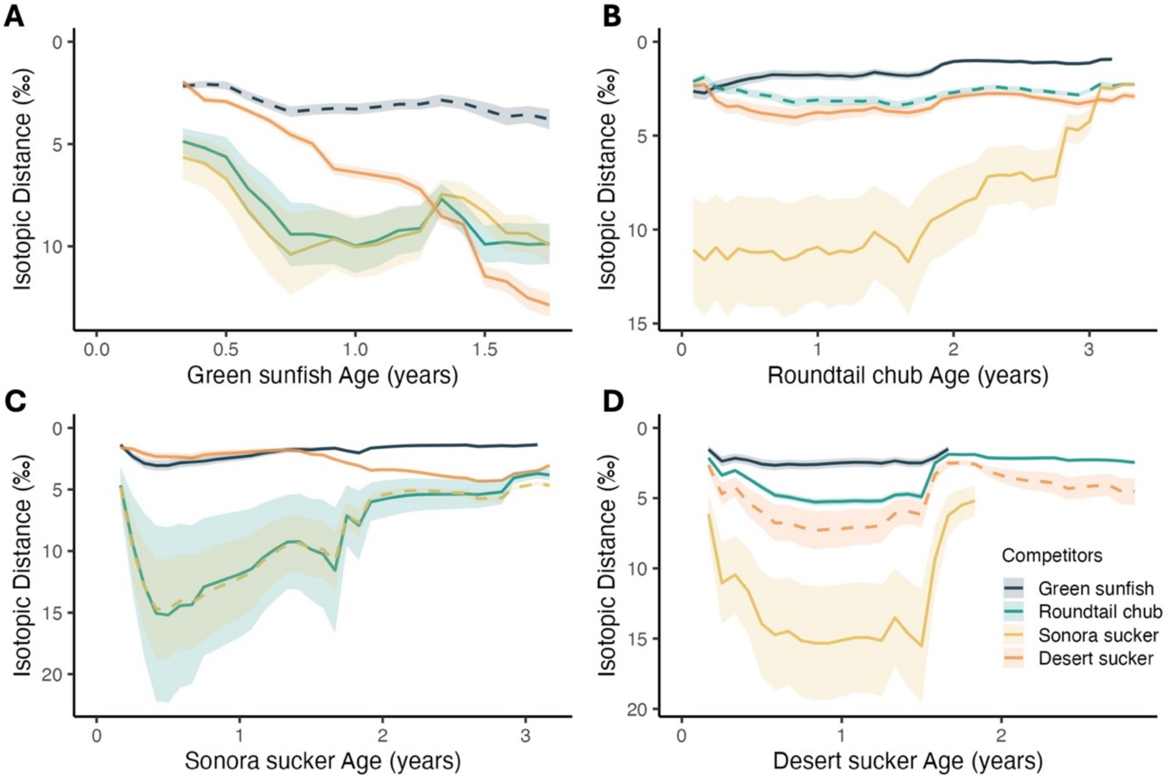

Figure 2.4: Mean isotopic distance (+/- standard error) from competitors across focal species age. Focal species displayed are green sunfish (A), roundtail chub (B), Sonora sucker (C), and desert sucker (D), with isotopic distance averaged across all ages of competitors for each monthly increment of the focal species age. Isotopic distance is defined as the squared Mahalanobis distance (D^2), which measures the distance from an individual point to the centroid of the competitor's isotopic niche in C-N biplot space. Low numbers indicate high isotopic niche overlap. Dashed lines represent intra-specific comparisons, and solid lines represent inter-specific comparisons.

Figure 2.5: Heatmap representing the rate of change in isotopic distance through ontogeny between focal species – competitor species pairs using biased random walk models. Isotopic distance is defined as the squared Mahalanobis distance (D^2), which measures the distance from an individual point to the centroid of the competitor's isotopic niche in C-N biplot space.

2.9 APPENDIX 2

Table A2.1: Sample size, length and age ranges, and trophic guilds of fish species captured from Burro Creek, Arizona.

Species	**Sample size**	**Length range (mm)**	**Age range (yrs)**	**Trophic Guild**
Green sunfish	63	64-167	1-3	Invertivore shifting to piscivore
Roundtail chub	67	73-223	1-6	Invertivore shifting to piscivore
Sonora sucker	56	82-335	1-6	Primarily invertivore
Desert sucker	58	87-203	1-5	Primarily herbivore, also invertivore

Table A2.2: Physidae snail baseline stable isotope ratios at each sampling location in Burro Creek, Arizona.

Sampling Location	**Nested Site**	$^{13}C/^{12}C$	$^{15}N/^{14}N$
CO-1	site 1	0.0108477	0.0036964
	site 2	0.0108318	0.0037012
FR-1	site 1	0.0108044	0.0036993
	site 2	0.0108428	0.0036871
FR-2	site 1	0.0108930	0.0037016
	site 2	0.0109126	0.0037034
BU-1		0.0108670	0.0036834
BU-2		0.0108807	0.0036935
BU-3		0.0108903	0.0036839
BU-4		0.0108933	0.0036846
BU-5		0.0108491	0.0036832
BU-6		0.0108896	0.0036994

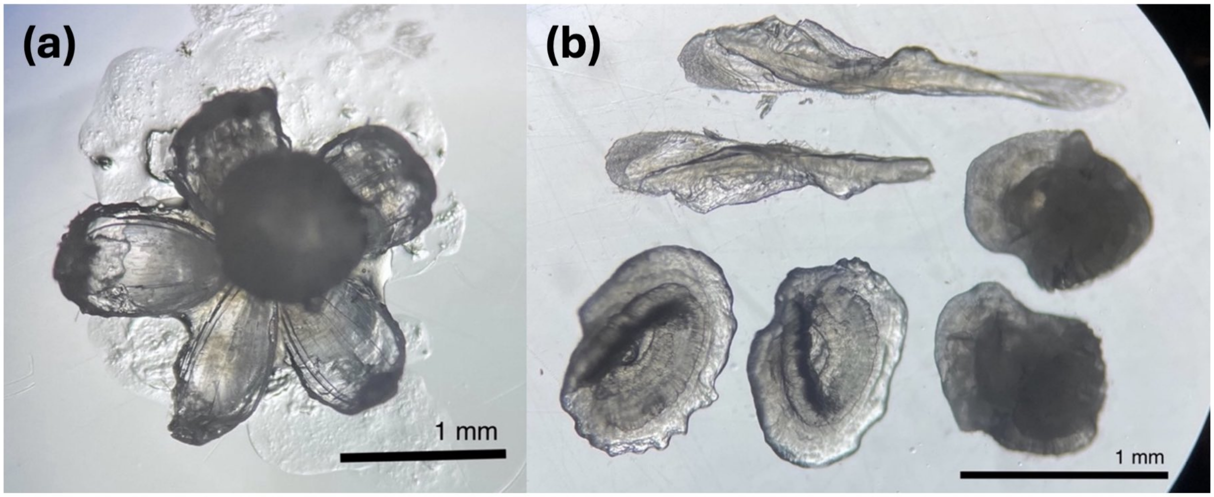

Figure A2.1: Fish eye lens delamination under the microscope (a) and desert sucker otoliths clockwise from top: sagittae (smaller one is broken), lapilli, and asterisci (b). Photo credit: Jessica Diallo.

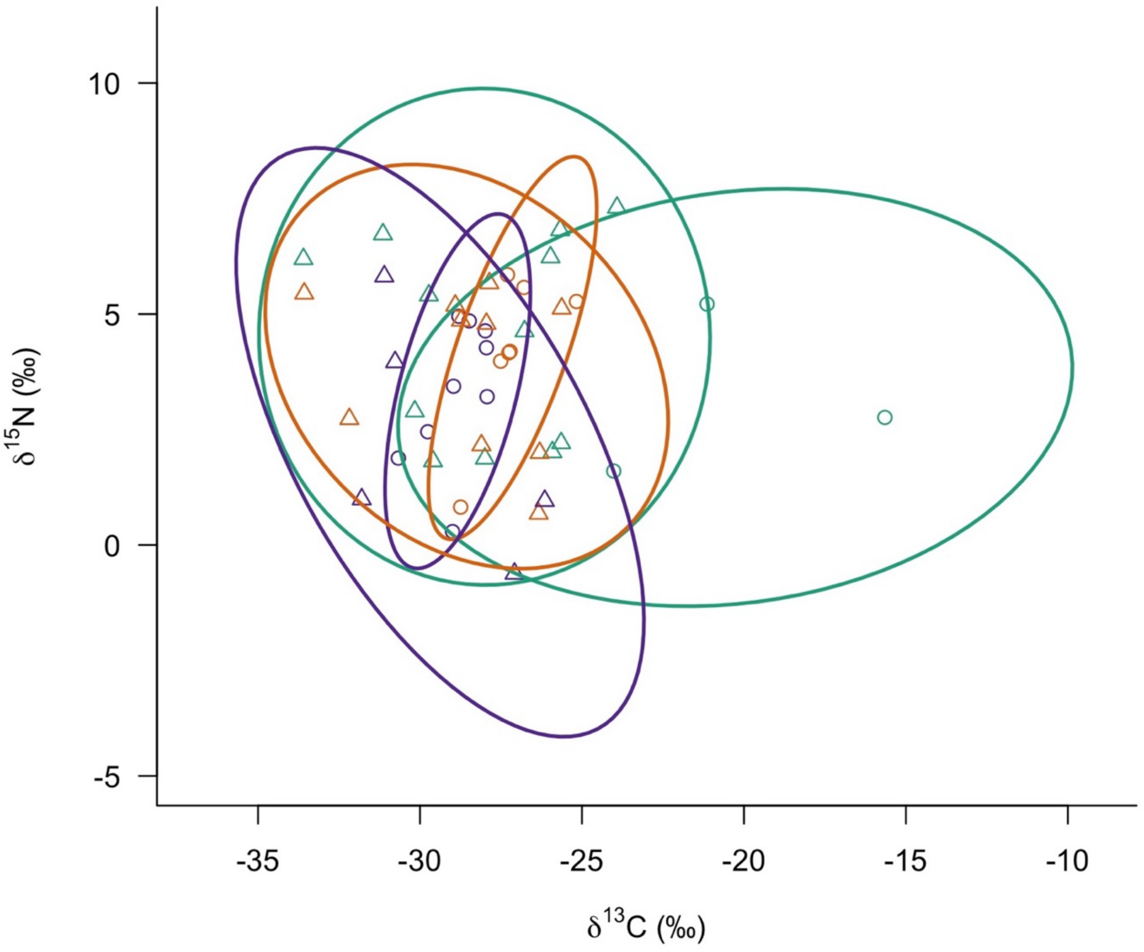

Figure A2.2: Stable isotope values (δ^{13}C and δ^{15}N) and prediction ellipses (95% confidence level) of macroinvertebrates in Burro Creek, Arizona, between 2016 (circles) and 2021 (triangles). Macroinvertebrate families displayed are Simuliidae larvae (orange), Baetidae larvae (purple), and Physidae snails (green). Units are per mil relative to international standards (Vienna Pee Dee Belemnite for δ^{13}C and air for δ^{15}N).

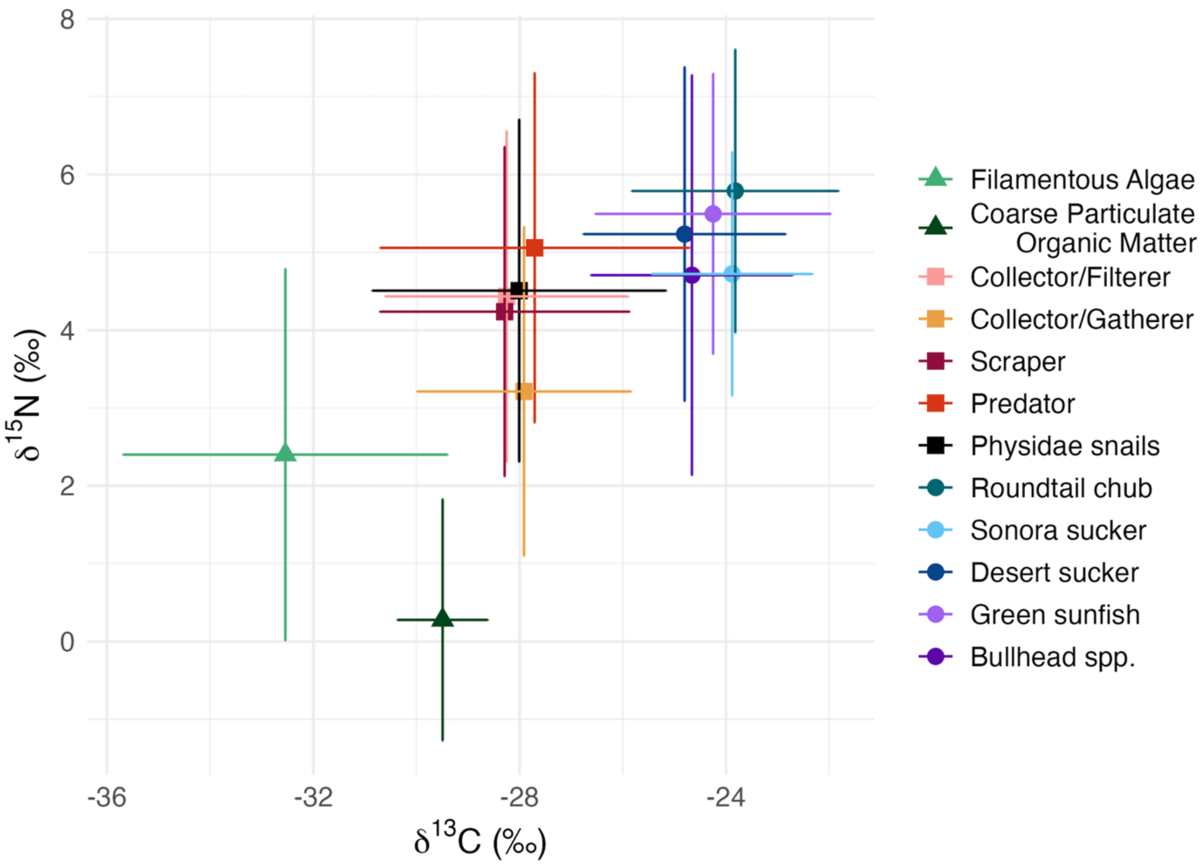

Figure A2.3: Stable isotope biplot displaying the food web structure in Burro Creek, Arizona. The mean across sites is displayed with standard deviation error bars. Primary producers are filamentous algae (aquatic derived) and coarse particular organic matter (terrestrial derived). Aquatic macroinvertebrate stable isotope values are separated by functional feeding group for the 10 most common families: collector/filterer (Simuliidae, Philopotamidae), collector/gatherer (Baetidae, Chironomidae, Leptohyphidae), scraper (Heptageniidae, Physidae), and predator (Coenagrionidae, Corydalidae, Tabanidae). Physidae snails are also displayed separately as the stable isotope baseline used to standardize fish eye lens values across sites. Fish eye lens tissue is used to represent the different fish species (lens stable isotope data first averaged within individuals, then each site). Units are per mil relative to international standards (Vienna Pee Dee Belemnite for δ^{13}C and air for δ^{15}N).

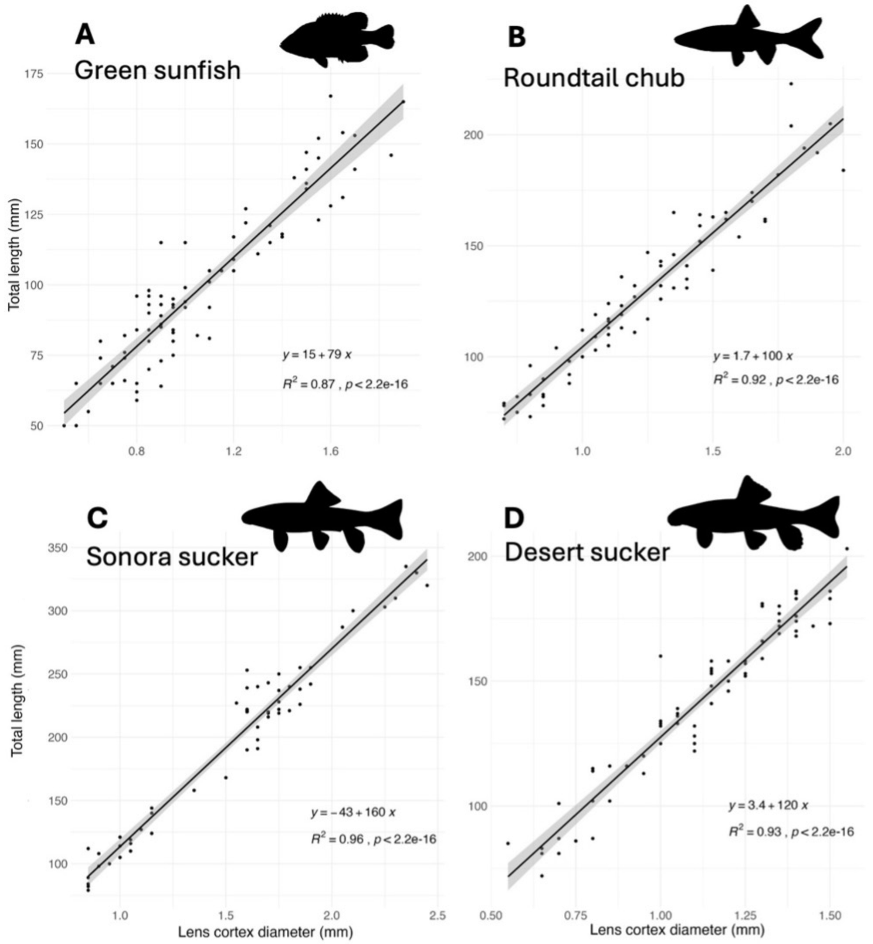

Figure A2.4: Total length vs. lens cortex diameter linear regression for green sunfish (A), roundtail chub (B), Sonora sucker (C), and desert sucker (D).

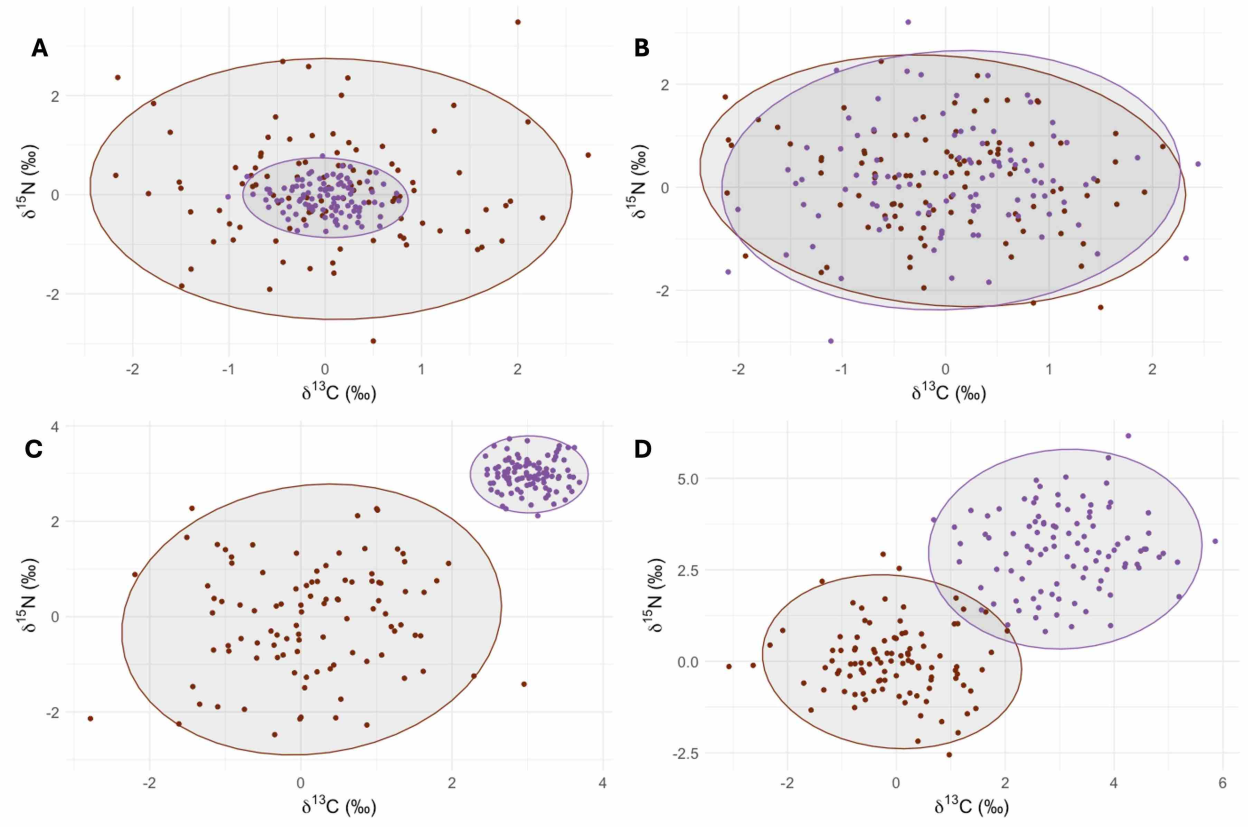

Figure A2.5: Possible outcomes of intra- and inter-specific comparisons between two species, displayed in δ^{13}C - δ^{15}N isotopic space (randomly generated data). Brown points represent species 1 and purple points represent species 2. Isotopic distance is defined as the squared Mahalanobis distance (D^2), which measures the distance from an individual point to the centroid of the competitor's isotopic niche in C-N biplot space. In panel A, intra-specific > inter-specific mean isotopic distance for species 1 and inter-specific > intra-specific mean isotopic distance for species 2. In panel B, intra-specific = inter-specific mean isotopic distance for both species. In both panels C and D, intra-specific > inter-specific mean isotopic distance for both species.

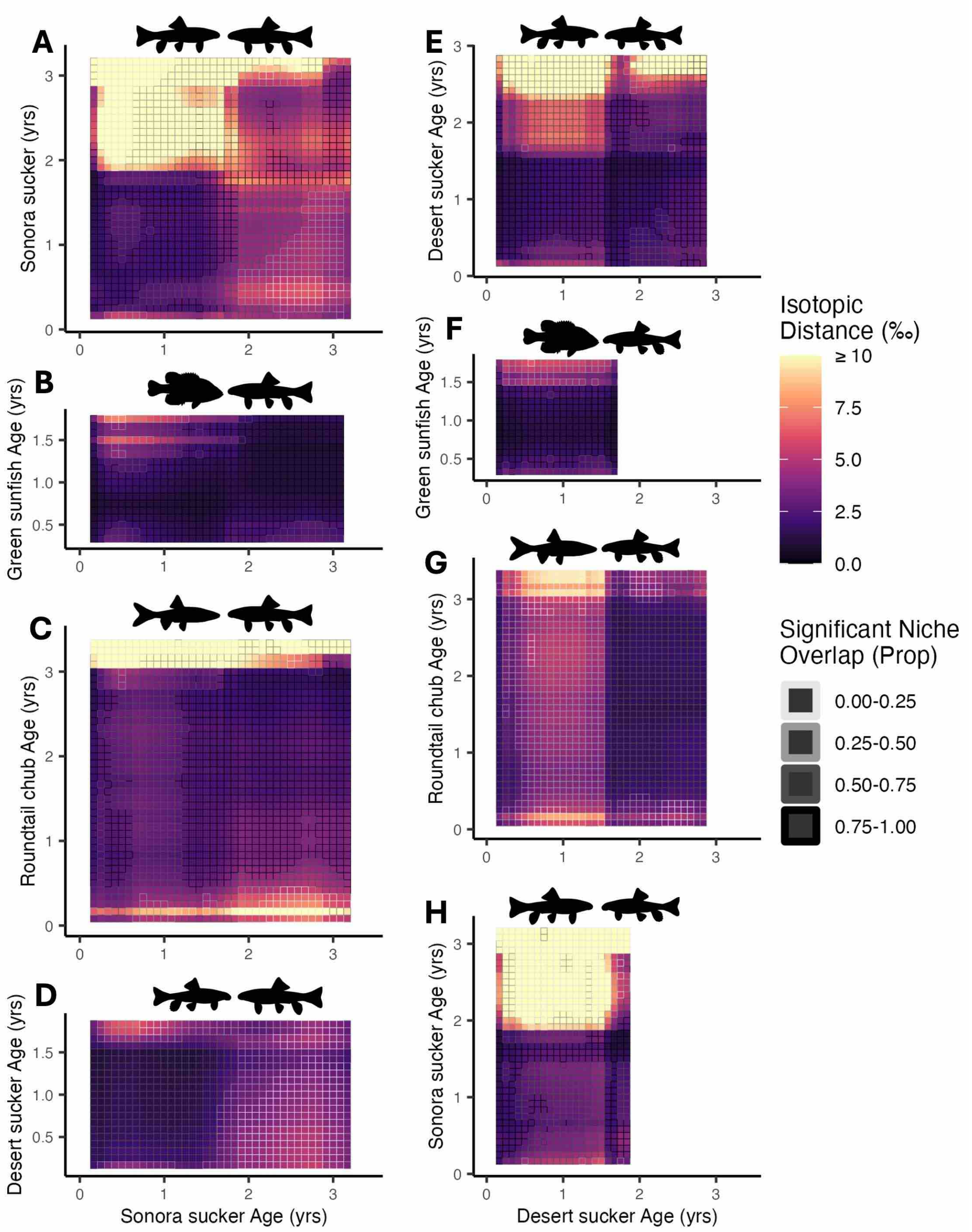

Figure A2.6: Competitive interaction surface displaying isotopic distance across the lifetimes of focal species Sonora sucker (plots A-D) and desert sucker (plots E-H) with competitors. Isotopic distance is defined as the squared Mahalanobis distance (D^2), which measures the distance from an individual point to the centroid of the competitor's isotopic niche in C-N biplot space. Interaction squares are outlined a shade of grey representing significant niche overlap, or the proportion of the focal species individuals that significantly overlap with the competitor's isotopic niche based on a chi-square distribution. Fish silhouettes display the competitor on the left, focal species on the right (not to scale).

Chapter 3. OPTIMIZING CONTROL OF A FRESHWATER INVADER IN TIME AND SPACE

Publication history: This study was co-authored with Sarah J. Converse, Matthew Chmiel, Andrew J. Stites, and Julian D. Olden. This chapter has been published in *Ecological Applications* (citation below).

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3.1 ABSTRACT

The global spread of invasive species in aquatic ecosystems has prompted population control efforts to mitigate negative impacts on native species and ecosystem functions. Removal programs that optimally allocate removal effort across space and time offer promise for improving invader suppression or eradication, especially given the limited resources available to these programs. However, science-based guidance to inform such programs remains limited. This study leverages two intensive fish removal programs for nonnative green sunfish (*Lepomis cyanellus*) in intermittent streams of the Bill Williams River basin in Arizona, USA, to explore alternative management strategies involving variable allocation of removal effort in time and space and compare static versus dynamic decision rules. We used Bayesian hierarchical modeling to estimate demographic parameters using existing removal data, with evidence that both removal programs led to at least a 0.39 probability of eradication. Simulated alternative management strategies revealed that population suppression, but not eradication, could be achieved with reduced effort, and that dynamic management practices that respond to species abundance in real time can improve the efficiency of removal efforts. High removal frequency and program duration, including continued monitoring after zero fish were captured, contributed to successful population control. With management efforts struggling to keep pace with the rising spread and impacts of invasive species, this research demonstrates the utility of

quantitative removal models to help improve invasive removal programs and robustly evaluate the success of population suppression and eradication.

3.2 INTRODUCTION

Invasive species are a persistent and growing threat to biodiversity and ecosystem function (IPBES 2023). In freshwater environments, the consequences of fish introductions can be severe and range from behavioral shifts in native species or changes in gene expression and hybridization, to the complete restructuring of freshwater food webs and the extirpation of entire faunas (Cucherousset and Olden 2011; Gallardo et al. 2016). The growing magnitude of these impacts, and increased awareness by society, have sparked action by natural resource agencies to suppress or eradicate some populations of invasive fish. The fundamental goals of these control programs often include protecting threatened native fishes and restoring critical ecosystem functions. Management approaches are diverse, including mechanical removal of individuals (Knapp and Matthews 1998), application of chemical piscicides (Gresswell 1991), introduction of biocontrol agents such as predators (Davies and Britton 2015) or pathogens (McColl, Sunarto, and Holmes 2016), and genetic manipulation to inhibit reproduction (Raschka et al. 2018).

Mechanical removal is the most common approach to invasive fish control (Rytwinski et al. 2019). Methods include gill netting, electrofishing, hook-and-line angling, as well as active (e.g., seine) and passive (e.g., hoop and minnow traps) trapping. Following a long history of stocking for recreational fishing, for example, brook trout (*Salvelinus fontinalis*) were successfully eradicated using intensive gill netting from high elevation lakes in the Sierra Nevada mountains of the United States (Knapp and Matthews 1998) and the Italian Alps (Tiberti et al. 2019). Exhaustive gill netting and trapping were also used to eradicate invasive spotted bass (*Micropterus punctulatus*) from a South African river (van der Walt et al. 2019). Mechanical removal enables more targeted removal of invasive species, and is often favored over piscicide chemical treatments that are more effective at eradicating invasive fish (Rytwinski et al. 2019) but are associated with environmental concerns, including potential harm to non-target species when broadly applied (Britton, Davies, and Brazier 2010).

Despite some documented successes, mechanical removal of invasive fishes has overall produced mixed management outcomes. In cases where eradication was the objective, just over half (58%) of documented cases achieved that goal (Rytwinski et al. 2019). Mechanical removal for population suppression has also produced varied results depending on removal methods, with electrofishing reducing population sizes in 44% of attempts (Rytwinski et al. 2019). Eradication or suppression failure may be related to large population sizes (Syslo et al. 2011), reinvasion of target species (Rytwinski et al. 2019; Dunham et al. 2020), ecological release from predators or competitors in their native range (Syslo et al. 2020), and compensatory increases in density-dependent populations (Meyer, Lamansky, and Schill 2006; Zipkin et al. 2009; Weber et al. 2016). For example, population suppression was initially unsuccessful for invasive lake trout (*Salvelinus namaycush*) in Yellowstone Lake, following the removal of nearly half a million individuals from 1995-2009 (Syslo et al. 2011). After increasing suppression effort, there was a decline in total lake trout abundance and biomass from 2012-2019 (Koel et al. 2020). In the upper Colorado River basin, populations of northern pike (*Esox lucius*) continued to increase between 2004-2010 despite the removal of 4,898 pike over that 7-year period because recruitment and immigration outpaced removal and natural mortality (Zelasko et al. 2016).

Positive management effects on native species and ecosystems can occur when suppression of invasive fish populations is successful, even without complete eradication. In situations where eradication is unlikely or too expensive, initiating harvest of nonnative predators at high densities may be a cost-effective suppression strategy because removal targets can be achieved with less effort and predation on the prey population can be lessened considerably (Baxter et al. 2008; Pasko and Goldberg 2014). In response to a 90% reduction of nonnative smallmouth bass (*M. dolomieu*) abundance in an Adirondack lake, native fish abundance increased by 4-90 times within two years, due to reduced predation (Weidel, Josephson, and Kraft 2007). The suppression of invasive sea lampreys (*Petromyzon marinus*) in the Laurentian Great Lakes has used a maximum acceptable number of sea lamprey wounds on native lake trout as a suppression target, in addition to sea lamprey abundance. This benchmark promotes native lake trout recovery since wound rate is an approximate measure of sea lamprey-induced mortality (Treska et al. 2021). For invasive populations that are closely monitored, achieving functional eradication – referring to reducing an invasive population below a threshold that causes undesirable effects (Green and Grosholz 2021) – can increase the efficiency of resource allocation.

A persistent challenge in invasive species control is deciding how to distribute removal effort (Myers et al. 2000; Zavaleta, Hobbs, and Mooney 2001; Prior et al. 2018). Quantitative models are playing an increasingly central role in guiding the optimal allocation of invasive species removal effort in time and space, identifying efficient removal methods, and estimating eradication success (Thompson, Olden, and Converse 2021). Models informed by past removal data can be used to evaluate resource allocation options and identify management strategies that result in preferred tradeoffs between higher probability of eradication and lower resource expenditure (Yackel Adams et al. 2024). Management simulations of invasive grass carp (*Ctenopharyngodon idella*) led to the conclusion that targeting centrally located populations, rather than the invasion front, was more effective in reducing the risk of spread throughout the continental United States (Erickson et al. 2018). In another case, a hierarchical demographic model was used to determine that intensive control prior to spawning and juvenile dispersal would be the most effective strategy for controlling northern snakehead (*Channa argus*) in the Potomac River (Jiao et al. 2009). Removal models have demonstrated utility for estimating abundance based on the number of individuals removed from a population (Rodriguez De Rivera and McCrea 2021), resulting in increasing application across diverse taxonomies including mammals (Davis et al. 2016), reptiles (Link et al. 2018; Udell et al. 2022), and fishes (Tiberti et al. 2021). This class of abundance estimation models in which no animals are marked or recaptured is well suited to invasive species management because removal data are a natural byproduct of management actions, and the estimated residual population size provides a measure of removal success. In a recent application, Link et al. (2018) developed a Bayesian hierarchical model that estimates population abundance, growth, movement, and detection probability based on removal data. Demographic modeling from removal data offers a unique opportunity to retrospectively evaluate invasive species removal efforts and to allow for the comparison of alternative control actions to inform future management.

In response to multi-decadal declines in native fish species throughout the southwestern United States (Minckley et al. 2003), invasive species control is being applied more frequently by management agencies. These control efforts have sought to prevent spread, control population size, or eradicate isolated populations (Mueller 2005; Rogosch and Olden 2021). Centrarchids, in particular green sunfish (*Lepomis cyanellus*), have been identified as an invader of high concern due to their widespread distribution and negative impacts on native fish communities through competition and predation (Dudley and Matter 2000; Rogosch and Olden 2020). Several green sunfish removal programs have been established in the lower Colorado River basin and elsewhere with the goal of native fish conservation. Multi-year removal programs have been conducted by the Arizona Game and Fish Department (AZGFD) to eradicate green sunfish from Trout Creek tributaries of the upper Bill Williams River basin (BWRB). The goal of these programs is green sunfish eradication, rather than suppression, because of the high fecundity of green sunfish and small native fish populations that are at risk of local extirpation due to predation.

We evaluated the success of green sunfish removal programs in two upper BWRB tributaries, as measured by final population estimates. Bayesian hierarchical modeling was applied to extensive removal data to estimate demographic and management parameters. Those parameters were then used to simulate alternative management strategies involving variable allocation of removal effort in time and space. These alternative management strategies explored the relative effectiveness of static decision rules, where effort allocation is determined at the outset, versus dynamic decision rules, where effort allocation changes through time based on catch rate. The simulation outcomes were evaluated against a suppression target (< the starting population) and eradication target (< 2 fish). Results from our study demonstrate how removal models, coupled with simulation of removal programs, may lead to more efficient and effective allocation of limited resources in future invasive fish control programs.

3.3 METHODS

Study system: Upstream tributaries of the BWRB are hydrologically intermittent with isolated pools separated by dry reaches. These dry reaches act as semi-permeable natural barriers that prevent movement between pools and upstream recolonization for the majority of the year. East Ash Creek and McGee Wash, two tributaries in the upper BWRB (Fig. 3.1), provide important habitat for native roundtail chub (*Gila robusta*), Sonora sucker (*Catostomus insignis*), desert sucker (*Catostomus clarkii*), and speckled dace (*Rhinichthys osculus*; East Ash Creek only). At the time of removal program initiation, green sunfish were the only nonnative species to inhabit these tributaries. These streams were chosen for green sunfish removal because reinvasion was deemed unlikely due to their intermittency and disconnection to the downstream sections.

Fish removals: Collection methods involved backpack electrofishing, beach-seining, minnow trapping, hoop netting, and hook-and-line angling; all of these methods have previously been applied in other fish eradication programs (Rytwinski et al. 2019). Backpack electrofishing was conducted with an LR 24 Smith-Root backpack electrofisher or a Halltech HT2000 BMK5 electrofisher set at 150-250 V and 60-80 Hz. The seine was 3 m x 1.2 m with 3.175 mm (1/8 inch) mesh. Minnow traps were collapsible Promar or Gee brand traps of either double throat 0.85 m length x 0.3 m diameter with 9 mm mesh or 0.46 m length x 0.25 m square diameter with 1.6 mm mesh. Hoop nets were two-hoop, single throat, with 0.52 m diameter, 1.0 m length, and 0.6 cm mesh. Both hoop nets and minnow traps were baited with fish chow. Angling data were not considered further because only 25 and 121 individuals were collected from McGee Wash and East Ash Creek, respectively, using this method. Removal with a combination of gear types progressed from downstream to upstream in a pass. Gear types used for removal were chosen in part based on time of year and pool habitat conditions (i.e., placing hoop nets in pools large enough to accommodate them). Hoop nets and minnow traps were combined into a single passive trapping method. When multiple gear types were used during a removal event, the order of deployment was invariably seining first, then hoop netting/minnow trapping (either set for 4 hours on single day trips or set overnight for 12 hours on multiple day trips), and last, electrofishing.

Green sunfish removals were conducted in East Ash Creek and McGee Wash between 2013 and 2021. The McGee Wash removal of 13,794 green sunfish within a 1.6-km reach of 26 sites occurred over 49 removal events between August 2017 and July 2021 (Fig. 3.2A). In a 2.5-km reach of East Ash Creek with 39 sites, the removal of 1,696 green sunfish occurred over 18 events between November 2013 and May 2015 (Fig. 3.2B). No green sunfish were captured during the last five removal events in East Ash Creek up to May 2015 and McGee Wash up to July 2021. As of those dates, the intensive removal programs were considered complete by the AZGFD, although monitoring has continued at these sites. Removal events were trips lasting 1-3 days and occurring, on average, every 31 days (range: 6 to 106 days). Green sunfish were humanely euthanized when captured, and all native fishes were returned alive to the stream.

Model structure: Green sunfish removal data were analyzed in a modeling framework with a dynamic removal model and a population growth model (Fig. 3.3), based on Link et al. (2018). Abundance was modeled as spatially explicit, and individuals were separated into two size classes. A visit to a stream constituted one removal "event," i.e., a single primary occasion. In a few cases, visits that occurred within a 13-day period were combined into the same removal event (resulting in 42 removal events in McGee Wash; 17 for East Ash Creek). In each removal event, the multiple removal methods constituted secondary occasions, providing the information necessary to separate capture probability and abundance (i.e., analogous to the capture-recapture robust design method (Kendall, Pollock, and Brownie 1995)). When removal events were combined, the secondary removals by gear type were kept separate and occurred in order of date and gear type (e.g., Date 1 seining, Date 1 trapping, Date 1 electrofishing, Date 2 seining, Date 2 trapping, Date 2 electrofishing). We assumed no births or deaths occurred within the short time duration of the removal events (i.e., only removals modify abundance), but allowed for population growth between removal events. We did not incorporate fish movement into the model given that the pools (i.e., sites) were separated by dry stream reaches that only connect during heavy rainfall events.

We distinguished two size classes, juveniles (< 50 mm) and adults (≥ 50 mm), based on the total body length at maturity estimated by Moyle (2002) and Rogosch et al. (2019). We accounted for separate size classes throughout the modeling process for the purpose of modeling stage-specific population growth. Capture probability varied by removal method, but we assumed equal capture probability by size class within each removal method. This assumption of equal capture probability by size class holds true where data are available (Price and Peterson 2010).

The Bayesian modeling approach provided a posterior distribution of the final population size, summed across size class and site, as a quantitative measure of success that could be used to inform decision making (i.e., whether to continue investing time and resources in removal). We characterized the probability of successful eradication as the probability that the final population size was < 2 individuals.

We estimated site-specific abundance based on removal data, where N_{kitj} is the abundance and Y_{kitj} is the number removed, indexed by $k = 1, \ldots, K$ size classes, $i = 1, 2, \ldots, I$ sites; $t = 1, 2, \ldots, T$ primary removal events; and $j = 1, 2, \ldots, J$ gear types, or secondary removal events. We modeled the data as

$$(1) \qquad Y_{kitj} \sim \text{Binomial}\,(N_{kitj}\,, p_{itj}),$$

where p_{itj} is the capture probability for an individual at site i during removal event t for gear type j. Capture probability, p_{itj}, is modeled as

$$(2) \qquad \text{logit}(p_{itj}) = \alpha_j + \beta * \log(\xi_{itj}),$$

where ξ_{itj} is effort. We estimated a separate intercept, α_j, for each gear type but we modeled the effect of effort, β, as constant across gear types because data were not sufficient to estimate β based on gear type. We standardized removal effort between 0 and 1 for each gear type using empirical cumulative distribution functions. Following removal by each gear type, the population available for removal from the next gear type is obtained via subtraction as

$$N_{kit(j+1)} = N_{kitj} - Y_{kitj}. \tag{3}$$

After the removal event (i.e., after application of the final gear type, J, within removal event t), the total population size remaining is also obtained via subtraction as

$$R_{kit} = N_{kitJ} - Y_{kitJ}. \tag{4}$$

The post-removal population is allowed to grow according to a discrete-time stage-based population growth model (Lefkovitch 1965) with demographic stochasticity included via Poisson random variation. The stage-based transition matrix is based on the number of days between removal periods and differs for post-spawning population increase periods compared to the rest of the year. Each size class, represented by $k = 1, 2$, has parameters for transition probabilities incorporating daily mortality, s_k, raised to the power of the number of days between removal events, and adults, $k = 2$, have an additional fecundity parameter that varies by year, f_y. The addition of juveniles to the population available for removal occurs in the model at one time per year, immediately after the first removal event in June. Peak spawning occurs in mid-May (Moyle 2002). Therefore, using June as the post-spawning population increase period in the model is based on a conservative estimate for when eggs will have hatched and juveniles will have grown large enough to be captured. We also assumed that juveniles hatched the previous year will grow to be ≥50mm by June, thus meeting the size threshold for adults and transitioning into the adult size class at the same time as the post-spawning population increase. Population growth, following removal, results in the new population size for each site $N_{ki(t+1)1}$. During non-growth time periods, population change for both size classes $k = 1$ and $k = 2$ is modeled as

$$N_{ki(t+1)1} \sim \text{Poisson}(s_k^{Days} * R_{kit}) \tag{5}$$

where $Days$ is the number of days elapsed between t and t+1. In June, when new juveniles enter the modeled population and existing juveniles transition to the adult age class, population growth is modeled as

$$N_{1i(t+1)1} \sim \text{Poisson}(f_y * R_{2it}) \tag{6}$$

for juveniles and as

(7) $$N_{2i(t+1)1} \sim \text{Poisson}(s_2^{Days} * (R_{1it} + R_{2it}))$$

for adults.

Model priors and fitting: Parameter priors for the McGee Wash and East Ash Creek analyses are provided in Appendix 3: Table A3.1. In the McGee Wash model, s_k, f_y, α_j, and β priors were given minimally informative priors. The same priors in the McGee Wash model were used in the East Ash Creek analysis, except for α_j and s_k; estimating these parameters benefited from using priors based on the posterior probability distributions from the McGee Wash analysis. This was due to the McGee Wash analysis including more informative data (a longer time period, more gear methods used, and more fish removed). These removal programs occurred less than 10km away from each other in similar environments, justifying use of priors from one dataset in the analysis of the other dataset.

Initial population estimates in both models were separated by site and size class. Priors for the initial population abundances were discrete uniform distributions ranging between ΣY_{kitj} and $\Sigma Y_{kitj} + 700$, where t = 1-10 in McGee Wash (t = 1-7 in East Ash Creek) and j = 1-3 (i.e., ΣY_{kitj} is the sum of fish caught before the first post-spawning population increase). Thus, we allowed for the possibility that we missed up to 700 fish of each size class at each site prior to the first post-spawning population increase after the start of data collection. This number, 700, was chosen because it is more than the highest number of fish removed from a single site, size class, and time.

Parameters α_j, β, f_y, and s_k were estimated by using Markov chain Monte Carlo (MCMC) sampling in JAGS (Plummer 2003). Three Markov chains of 50,000 iterations with a 20,000 iteration burn-in period were run in R using the packages rjags and jagsUI (Kellner 2019; R Core Team 2021). Model convergence was satisfactory if the Gelman-Rubin statistics (i.e., Rhat) values were less than 1.1 for all parameters (Gelman and Rubin 1992).

Simulations: The green sunfish population in McGee Wash was simulated over the same time period as the removal program using alternative management strategies. These simulations began with the initial estimated population at McGee Wash and simulated alternative management approaches to that which was deployed on the ground, thereby allowing us to evaluate whether eradication could have been accomplished with fewer resources. We used McGee Wash because of the overall greater strength of the dataset, which allowed us to simulate the system with less uncertainty. Decision rules were employed to simulate alternative temporal and spatial allocations of effort under 8 alternative management strategies that were either static (where effort allocation was determined at the outset) or dynamic (where effort allocation changed through time based on catch rate; Table 3.1). In addition, we simulated the same removal strategy as was applied on the ground. The median total population size of green sunfish remaining at the end of the simulated removal program was compared between strategies. Probabilities of achieving the suppression target (< the starting population size) and eradication target (< 2 fish) were calculated as the proportion of simulations out of 1000 that resulted in a final population below these values.

In the 8 types of management strategies we considered, spatial and temporal effort allocation was reduced, compared to the true effort expended in the real removal program. The static strategies that reduced spatial allocation of effort involved (1) selecting a random subset of all sites, (2) selecting a random, contiguous, subset of all sites, or (3) selecting a subset of sites based on habitat volume. Temporal effort, or the number of removal events, was reduced in static strategies by (4) reducing the number of simulated removal events (i.e., removing less frequently), (5) reducing the number of simulated removal events while prioritizing pre-spawning removals, or (6) conducting simulated removal events for a shorter time period. Dynamic decision rules altered both spatial and temporal effort allocation by (7) removing from a subset of sites based on antecedent catch rates, or (8) terminating removal efforts at a site once fish were no longer captured.

For each management strategy, we simulated the population forward in time. The removal process was modeled as a binomial distribution as in equation (1) with abundance (N_{kitj}) beginning with the estimated starting abundance for each site and size class at $t = 1$ and $j = 1$ and capture probability (p_{ijt}) estimated by the model at each site, gear type, and removal event. Capture probability (incorporating α_j, β, and effort) was not manipulated in simulations because decisions regarding the level of effort expended were made in the field based on local conditions (e.g., water level and pool shape). An additional reason for not manipulating capture probability was that we found no relationship between effort and harvest rate (i.e., catch divided by estimated abundance; Appendix 3: Fig. A3.1).

The population growth process was simulated via the Lefkovich matrix based on the time between removal events, as in equations (5-7), but population growth was simulated without stochasticity via the Poisson distribution. When simulating the true effort allocation strategy, deterministic population growth resulted in an average outcome closer to the model estimate of reality, compared to stochastic population growth simulation outcomes. The fecundity parameter from the year 2018, f_{2018}, was used in simulations to allow for maximum reproduction observed in McGee Wash when the total population was at its highest, resulting in high population growth and conservative, worst-case removal scenario predictions. We ran the simulations including parametric uncertainty for the estimated life history parameters, s_k and f_{2018}. To accomplish this, we randomly selected an iteration from the MCMC chains and used the corresponding set of parameter estimates to run a single simulation forward in time. We then repeated this 1000 times for each simulation scenario. Because we were undertaking a simulation exercise meant to compare removal strategies, rather than an effort to accurately forecast total population size, survival and fecundity were not density dependent (i.e., infinite carrying capacity).

3.4 RESULTS

Estimates based on the green sunfish removal data indicated very low abundance in the two study streams following removal efforts. Initial populations at the start of the removal programs were estimated at 10,524 (95% BCI = 10,275-10,785) and 2,588 (95% BCI = 2,431-2,761) individuals, in McGee Wash and East Ash Creek, respectively. The final population estimate was 3 (95% BCI = 0-12) for both McGee Wash and East Ash Creek. In McGee Wash, the posterior distribution of the final population revealed a 0.398 probability of eradication (Fig. 3.4A). Spawning seasons in late spring led to population growth during 2018 and 2020, with estimated fecundity parameters of 19.3 and 16.2, respectively, in contrast with 2019 (0.487). Low abundance and few removal events following the 2021 spawning season results in reduced confidence in the 2021 fecundity estimate (9.27), but we found that outcome had little effect on abundance estimates or simulation results. The East Ash Creek final population posterior distribution resulted in a 0.399 probability of eradication (Fig. 3.4B). Estimated fecundity during 2014 in East Ash Creek was 0.312, similar to 2019 results in McGee Wash. Parameter posterior distributions and prior distributions used to inform both models are shown in Appendix 3: Table A3.1.

Model simulations point to the importance of spatial and temporal allocation of removal effort to achieve population control goals. Final populations across simulated management scenarios are displayed in Figures 3.5-3.8. For an example of a population time series during the simulated removal program, see Appendix 3: Fig. A3.2. The full effort management scenario led to a 0.92 probability of complete eradication (< 2 fish). Reducing effort spatially (fewer sites visited) or temporally (fewer removal events) resulted in higher final populations, with variable success in meeting the eradication and suppression targets.

Simulating reduced spatial allocation of effort in McGee Wash resulted in higher final populations compared with consistent removals from all 26 sites (100% pools chosen for removal; Fig. 3.5). Deploying removals in at least 50% of the sites (randomly selected during each removal event) was necessary to achieve population suppression, i.e., a median predicted final green sunfish population below the starting population (10,524) by the end of the program. When restricting removal effort to a subset of random contiguous sites, simulation results suggested that removals in at least 90% of sites were required to suppress the median final population below the starting population (Fig. 3.5). The probability of suppression reached 1.0 at 70% of sites randomly chosen for removal, compared with 100% of random contiguous sites. We believe this discrepancy between the randomly chosen sites compared to the random contiguous sites is due to pool 1 containing a large population of green sunfish. Pool 1 was excluded from most of the high percentage contiguous site selections due to its remoteness upstream, and as a result, there were fewer removals targeting that high abundance site. Selecting sites for removal based solely on pool volume (hypothesized to contain the greatest number of fish) produced similar results with less variability because the sites selected for removal were unchanged throughout the simulated removal program (Appendix 3: Fig. A3.3). In this case, removal effort in at least 90% of the largest sites was required for population suppression, but eradication was unlikely unless all pools were subject to removals.

Alternative temporal allocation of removal effort led to varied outcomes with respect to population control and eradication. Simulating 25 or more removal events (out of 42) led to population suppression with probability 1.0. When removals were less frequent than 20 over the course of the removal program, the final simulated population was larger than the starting population (Fig. 3.6). Prioritizing removal events immediately prior to spawning in May did not result in a significant benefit to the removal program. Implementing 25 out of 42 removal events led to a 1.0 probability of suppression and 0.0 probability of eradication. This increased to a 0.55 probability of eradication with 35 removal events. Simulating shorter removal programs resulted in a suppressed population when removal events lasted at least 18 months (Fig. 3.7). However, ending the removal program before it was nearly eradicated allowed the population to rebound. If the removal program had terminated after 24 months, when no fish were collected from all sites in McGee Wash for the first time, the model predicted that the green sunfish population would have subsequently grown to an estimated median 38 fish (95% CI: 0-481) by the end of the removal program almost two years later. The probability of eradication was 0.0 at 24 months, 0.15 at 30 months, 0.59 at 36 months, and 0.82 at 47 months.

Dynamic management in the simulated removals had demonstrated benefits with respect to population suppression. When the simulated removal program targeted sites with the highest number of fish captured based on an annually conducted removal event, the median final population could be reduced below the starting population with removal effort in 40% of sites (Fig. 3.8). As the percentage of sites with removal effort increased, the final simulated population declined. The probability of population suppression increased from 0.46 at 30% sites chosen for removal, to 0.95 at 40%, and 1.0 at 50% and higher. When 90% of sites were targeted for removal in this dynamic simulation strategy based on catch rate, the median final population was 89 fish (95% CI: 0-471) with 0.14 probability of eradication. Alternatively, discontinuing removals in sites after zero green sunfish were captured multiple times resulted in substantially reduced final population sizes relative to the starting population (Appendix 3: Fig. A3.4). When sites were no longer visited after zero fish were caught just once, the median final simulated population was 7,102 fish (95% CI: 2,719-15,335) with 0 probability of eradication. The probability of eradication increased to 0.30 (median 37 fish, 95% CI: 0-1,226) and 0.68 (median 0 fish, 95% CI: 0-248) at the end of the removal program when simulated removals ceased after zero fish were captured twice or three times, respectively. Finally, when all sites were consistently sampled in the simulation, the resulting probability of eradication was 0.92 (median 0 fish, 95% CI: 0-7).

3.5 DISCUSSION

An intensive fish control program was retrospectively examined to explore alternative management strategies in which spatiotemporal removal effort was allocated differentially in a stream ecosystem. Bayesian hierarchical model results revealed that the removal programs in the upper BWRB nearly eradicated invasive green sunfish populations. The probability of eradication (0.398 in both study systems) was remarkably alike between study systems that were both environmentally similar and subject to the same removal actions, but differed in initial population size. Even though the removal programs were conducted years apart, both implemented similar management decisions at the end of the removal program: sampling continued with four additional visits after zero total fish were caught. As demonstrated by simulations, extensive spatial effort was necessary for population suppression and high temporal effort allocation was required for population eradication. Although the simulations allowed density-independent population growth, our focus was on whether the suppression target (< the initial population abundance) and eradication target (< 2 fish) could be met at different removal rates.

Applying the removal model to two different streams and programs within the same watershed demonstrates the utility of the removal model. The McGee Wash removal program led to a well-informed model due to the high number of fish removed and longer time series. By contrast, the East Ash Creek removal program was shorter with fewer fish removed, and estimates benefited from informed parameter priors from the McGee Wash removal program. We could leverage data to understand population dynamics in a related system because these streams are geographically close, environmentally similar, and green sunfish were the target in both. Density dependence was not explicitly included in the Bayesian estimation model and we allowed fecundity to vary each year. During 2018 and 2020, the McGee Wash removal data displayed clear spawning peaks in which a high number of the juvenile size class were captured in the summer months. In East Ash Creek, few juveniles were captured in the summer of 2014, but their presence indicates that some spawning occurred. The McGee Wash removal data in 2019 did not include captured juveniles in between spawning seasons, leading us to believe that there was recruitment failure during that year. It is unknown whether this was due to the removal of thousands of adult green sunfish, however, the Allee effect and stochastic environmental dynamics (e.g., unfavorable streamflow) could have contributed to population eradication once the population was significantly reduced (Liebhold and Bascompte 2003).

Allocation of removal effort across space was the greatest determinant of the success of population suppression in our simulations, as reflected in the static spatial simulations. The relatively small size of isolated pools allowed managers to undertake removals in all of them, which also contributed to successful control. Our results support the long-held notion that fish eradication efforts via mechanical methods are more successful in relatively small, closed ecosystems, such as alpine seepage lakes (Knapp and Matthews 1998; Pacas and Taylor 2015; Tiberti et al. 2021) and isolated wetlands (Yick et al. 2021), where reinvasion is less likely. Although we did not model movement between sites due to knowledge of the system as isolated pools, the removal model could accommodate movement between sites (Link et al. 2018).

Including dynamic management in invasive species control leads to greater reductions in population size. Selecting McGee Wash sites for simulated removals randomly or based on pool size was not as effective as targeting removal efforts at sites with the highest catch rates. To suppress the final simulated population below the initial value required that at least 50% of sites were randomly sampled, but only 40% of sites needed to be sampled based on past catch rates, revealing a benefit of dynamic management. The results support the notion that learning from ongoing efforts and shifting expended effort in response to past removal rates can lead to more efficient population control. The suppression of invasive feral swine has benefited from a dynamic approach using removal data to estimate abundance and evaluate management effectiveness over time (Davis et al. 2022).

Successful control of the green sunfish population was enhanced by the high frequency of removal events. Without this investment in effort, model simulations suggest that the McGee Wash population of green sunfish would not have approached eradication. Evidence from other invasive fish species removal programs support this general finding. Annual removals of predatory invasive fishes from rivers have not achieved population suppression in many cases, despite multiple years of commitment (Meyer, Lamansky, and Schill 2006; Propst et al. 2015; Zelasko et al. 2016). Due to the relatively small spatial scope of the BWRB removal programs, frequent removals over the full spatial extent were achievable with available resources; however, this is not necessarily feasible with a larger or more complex study system. Simulating shorter program durations demonstrates the possible outcomes if a removal program does not have long-term funding and resources to sustain removal efforts; we saw clear trade-offs between the temporal allocation of removal effort and the level of suppression necessary for eradication.

A fundamental challenge of invasive fish control is deciding how to distribute removal effort in time and space, including when to claim eradication success and conclude management actions. This decision has implications for program cost, motivation of participants, and the assessment of perceived restoration benefits and minimizing unwelcome ecological impacts (Rout et al. 2014; Tiberti et al. 2021). If an eradication program is discontinued too early and the population rebounds, resources and time spent on suppressing the population will have been misplaced (Morrison et al. 2007). Effort misjudgment may also impact future control programs by affecting the confidence and trust of stakeholders (Estévez et al. 2015). Due to limited resources, control efforts cannot continue indefinitely, but terminating effort after an arbitrary "wait-and-see" period of time risks either eradication failure or wasted funds (Russell et al. 2017). However, imperfect detection can result in false declaration of eradication success after zero fish are captured for the first time. Our simulation results suggest that returning to sites after zero fish have been captured leads to greater probabilities of achieving eradication. This is a robust decision making rule employed in other cases that leads to more effective invasive species control in the face of uncertainty (Rout, Thompson, and McCarthy 2009; Rout et al. 2014).

Re-colonization of individuals from unmanaged areas is considered a primary contributor to the failure of invasive fish eradication programs (Rytwinski et al. 2019; Dunham et al. 2020), and eradication programs more broadly (Myers et al. 2000; Parkes and Panetta 2009). The upper BWRB tributaries in this study have semi-permeable natural barriers represented by dry intermittent stream reaches that prevent upstream recolonization into the removal areas in most, but not all years. In East Ash Creek where the intermittent reach is large (0.8 km), continued monitoring has revealed no reinvasion over the past seven years. However, in McGee Wash the natural barrier to recolonization is represented by a bedrock stream section that may be dry or have shallow flowing water. While revisiting McGee Wash in December 2021, five months after the control program concluded, additional green sunfish were captured in the most downstream sites. In December 2022, following strong monsoon flows that connected the stream for extended periods, green sunfish were captured throughout McGee Wash in low numbers. Continued monitoring of both upper BWRB streams will ensure that any reinvasion is detected early, and rapid management responses are implemented to prevent population re-establishment if possible. Permanent barriers to prevent recolonization of nonnative fishes are also possible, such as in the neighboring Gila River, Arizona, where concrete barriers were constructed prior to green sunfish eradication using piscicides (Clarkson and Marsh 2008). Population suppression to prevent population growth, rather than eradication, may be a better option in more connected ecosystems that are vulnerable to re-invasion (Baxter et al. 2008; Syslo, Guy, and Cox 2013).

Population suppression of invasive species may lead to native species recovery. This has been demonstrated in the Colorado River basin with the removal of multiple invasive fish species, although recovery success was also influenced by natural flow and thermal regimes (Coggins, Yard, and Pine 2011; Healy et al. 2020). Native species abundance has increased in response to the suppression of smallmouth bass (Weidel, Josephson, and Kraft 2007) and the local eradication of smallmouth bass and green sunfish (Marks et al. 2010). The green sunfish populations in these systems may not have been completely eradicated, but their populations were unequivocally suppressed to a large degree. It is unknown what level of green sunfish density in these streams would be low enough to result in minimal impacts to native species. However, there have been documented increases in native species populations in the East Ash Creek taking place after green sunfish removals, including roundtail chub, desert sucker, and Sonora sucker (Stites and Chmiel 2020). Future research could apply different suppression targets, linked to a native population response, within the simulation model to predict management outcomes as they relate to native species recovery.

Quantitative models of invasive species removal can inform the design of future management efforts. Our simulations illustrate the importance of extensive spatial effort for population suppression and frequent removals through time to achieve invasive fish population control in dryland streams. When applied to other species, the Bayesian modeling framework described here and in Link et al. (2018) can help managers make decisions about management under uncertainty, a key challenge in invasive species management. As relatively small, isolated ecosystems, dryland stream pools are similar to islands, which have a long history of invasive species control (Spatz et al. 2022). Quantitative models are increasingly being used to support invasive species control decision making on islands (Baker and Bode 2021; Zub et al. 2022), and those methods can be applied to other isolated ecosystems. Confidence in eradication can be achieved in these isolated ecosystems using quantitative tools to estimate the probability of species presence, the amount of monitoring required to reduce uncertainty, and the cost of falsely declaring eradication success (Ramsey, Parkes, and Morrison 2009; Ramsey, Anderson, and Gormley 2023; Rout, Thompson, and McCarthy 2009). Given limited resources by management agencies, efficient and effective use of resources is necessary to address the growing spread of invasive fish species.

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3.8 TABLES

Table 3.1: Simulated removal program strategies using McGee Wash estimated initial population, capture probability, and life history parameters. Each strategy reduced the spatial and/or temporal allocation of effort in either a static (consistent through time) or dynamic (changing through time and state-dependent) manner.

Removal program decision rules	**Simulated removal description**
Spatial (static)	Spatial allocation of effort was reduced, but temporal effort remained the same as in the true removal program.
Random sites	A subset of 10-100% of sites was randomly chosen for removal during each removal event. The random selection of sites was re-selected during each subsequent removal event.
Random contiguous sites	A subset of 10-100% of contiguous (i.e., adjacent to each other) sites was randomly chosen for removal during each removal event. The random selection of sites was re-selected during each subsequent removal event.
Largest sites (by volume)	A subset of 10-100% of sites selected for removal during each removal event was based on estimated habitat volume from pool measurements collected by the Arizona Game and Fish Department. The subset of sites chosen at each percentage was consistent through time because the rank of habitat volume between sites was assumed to remain constant despite possible changes in flow.
Temporal (static)	Temporal allocation of effort was reduced, but the spatial effort remained the same as in the true removal program.
Frequency of removal events	A subset of 5 - 42 (all) removal events was chosen. Removal events selected were approximately evenly spaced, although not exactly, because we restricted our simulations to removal event dates in the true removal program.
Frequency of removal events & prioritizing pre-spawning	A subset of 5 - 42 (all) removal events was chosen by prioritizing the selection of removal events during the pre-spawn month (April), rather than allowing the removal events to be equally spaced.
Duration of removal program	Early termination of the removal program by selecting a duration of the simulated removal program: 3 - 47 (all) months, and then allowing the population to continue to grow until the end of the simulated removal program (47 months).
Spatial & Temporal (dynamic)	Effort was re-allocated based on estimated state variables.

Sites with highest previous catch	A subset of 10-100% of sites was selected for removal based on catch rate during an annually conducted removal event. During one removal event per year (August, the time of the first removal event), all sites were selected for removal and ranked based on catch rate. Subsequent removal events selected the subset of sites with the highest number of fish removed according to ranking (top 10% - 100%). The following August, all sites were sampled again during a removal event, and a new ranking was created based on catch rate to define the subsets of sites.
Termination of removal according to fish detection	Fish removals were discontinued in sites that captured zero fish for one, two, or three removal events in a row. If any fish did remain in the sites with zero captures, that sub-population continued to grow until the end of the simulated removal program. These results were compared to a simulation in which removals continued in all sites regardless of the catch rate.

3.9 FIGURES

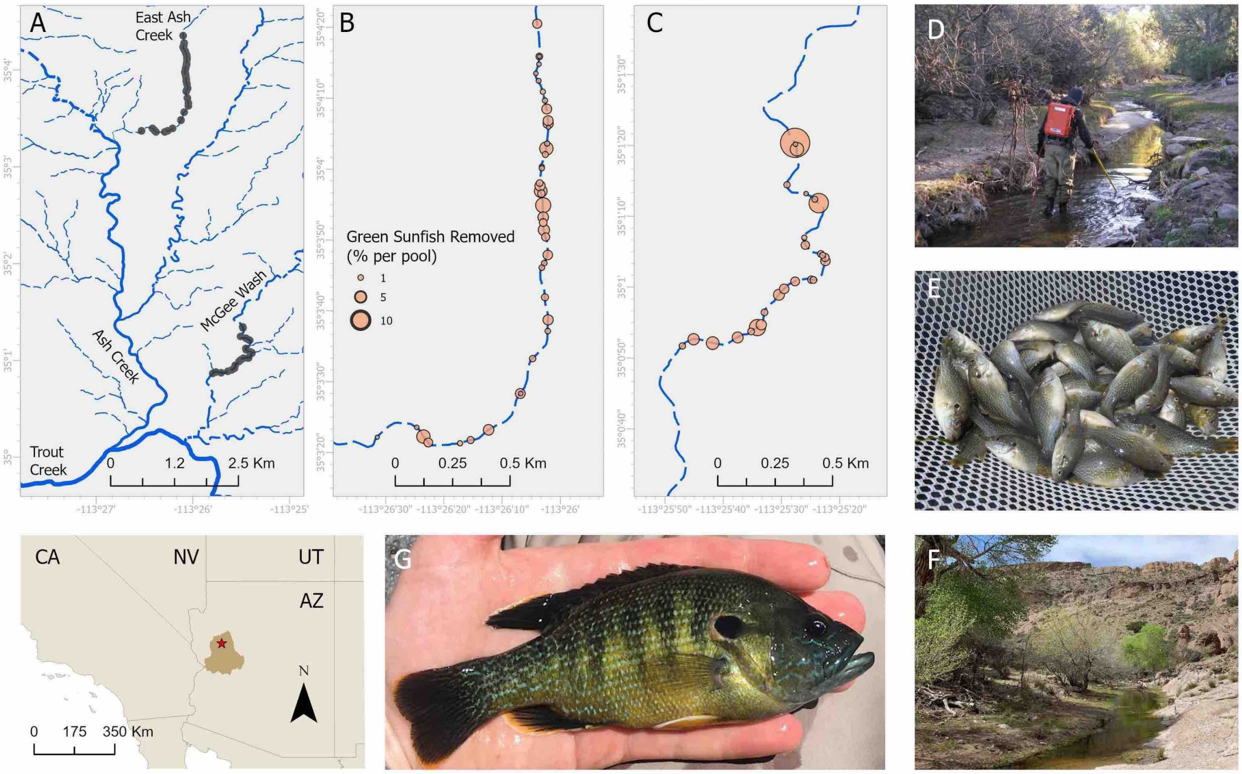

Figure 3.1: Map of tributaries within Trout Creek, AZ watershed where the Arizona Game and Fish Department (AZGFD) conducted green sunfish removals. Removal sites are identified by points. Panel A is the watershed including all removal sites, panel B is East Ash Creek, and panel C is McGee Wash. Panel D is AZGFD biologist David Partridge using a backpack electrofisher to remove fish from East Ash Creek (photo credit Gregg Cummins), panel E is a net full of green sunfish (photo credit Julian Olden), panel F is one of the pools in McGee Wash (photo credit Andy Stites), and panel G is a close up of a green sunfish caught in Burro Creek within the Bill Williams River basin, AZ (photo credit Jessica Diallo). Bottom left inset shows the greater region with the Bill Williams River basin in dark brown and a red star identifying the location of green sunfish removals.

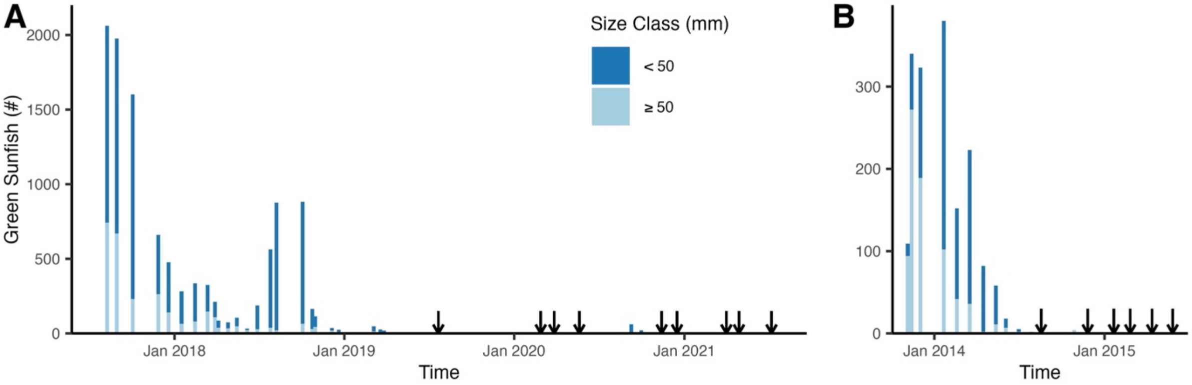

Figure 3.2: Green sunfish removed from McGee Wash (panel A) and East Ash Creek, AZ (panel B). Arrows indicate dates when zero fish were caught.

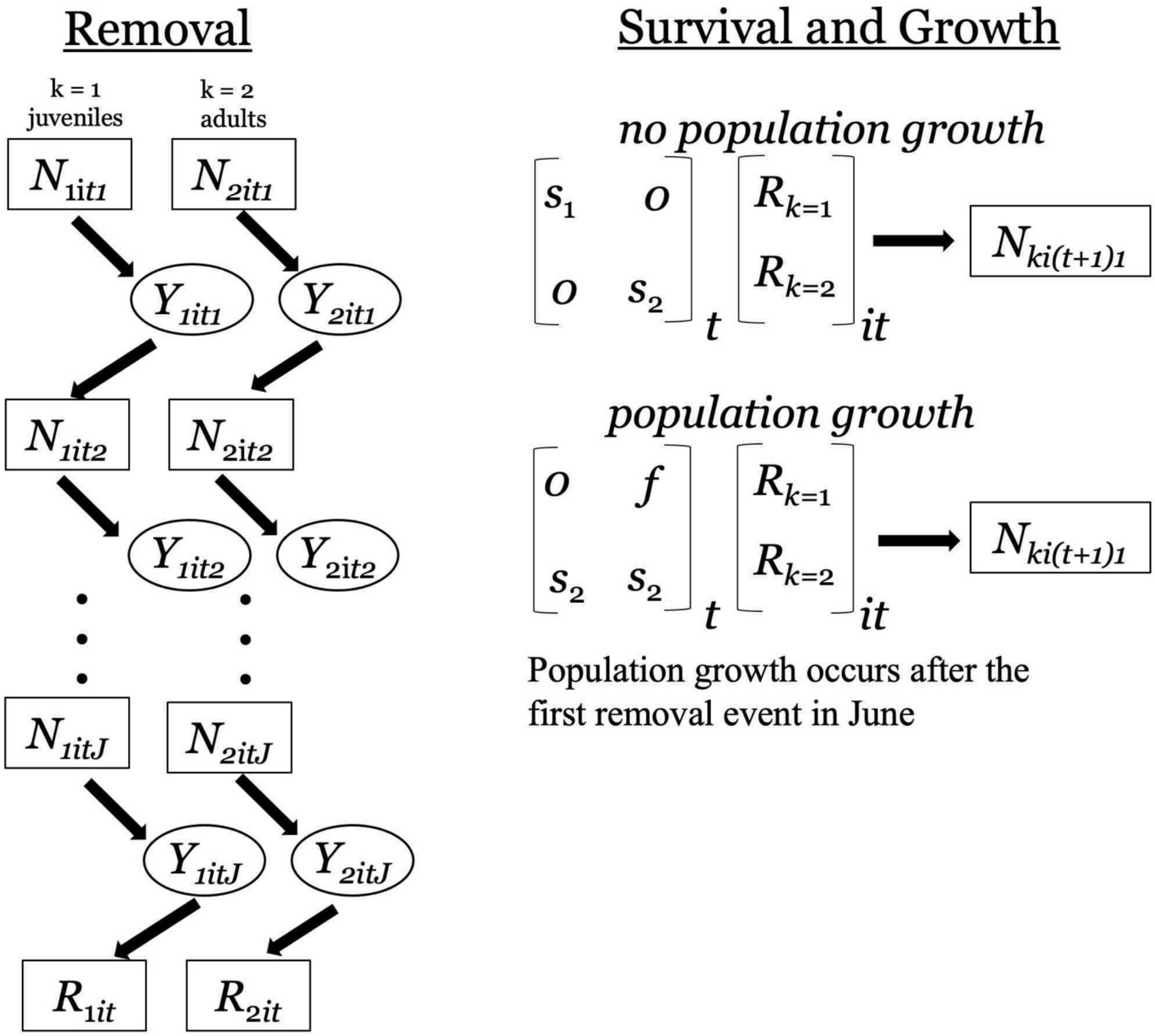

Figure 3.3: Model diagram for removal and population change of green sunfish in McGee Wash and East Ash Creek, AZ (size class k, site i, removal period t > 1, removal gear j). Rectangles are derived nodes and ovals are stochastic nodes. For model t = 1, N_{kit1} is stochastic.

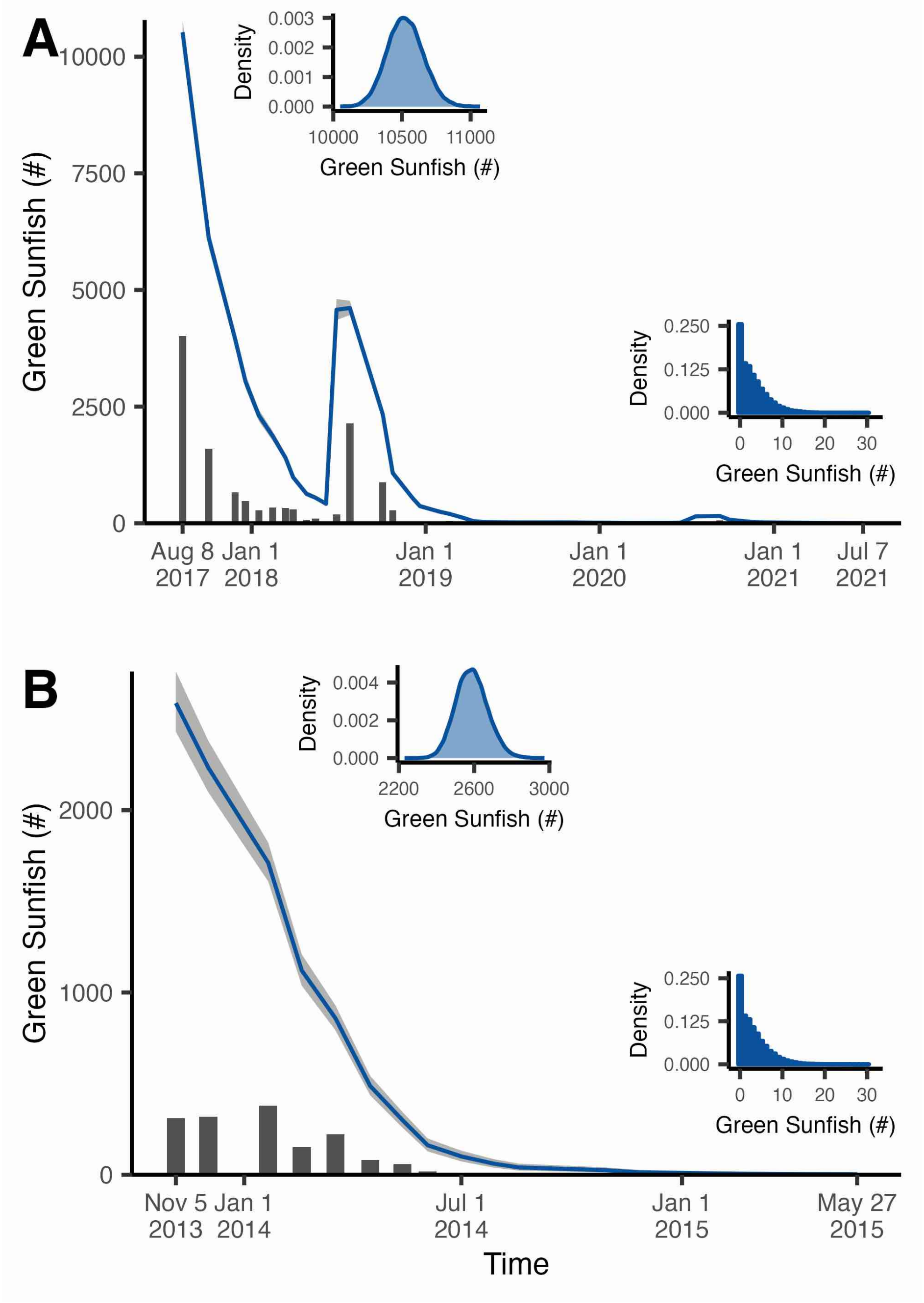

Figure 3.4: Model estimated green sunfish population (line) and number removed (grey bars) over time in McGee Wash (panel A) and East Ash Creek, AZ (panel B). Insets show posterior probability distributions of the total population at the start (upper left) and end (lower right) of the removal program. Grey ribbon represents the 95% credible interval.

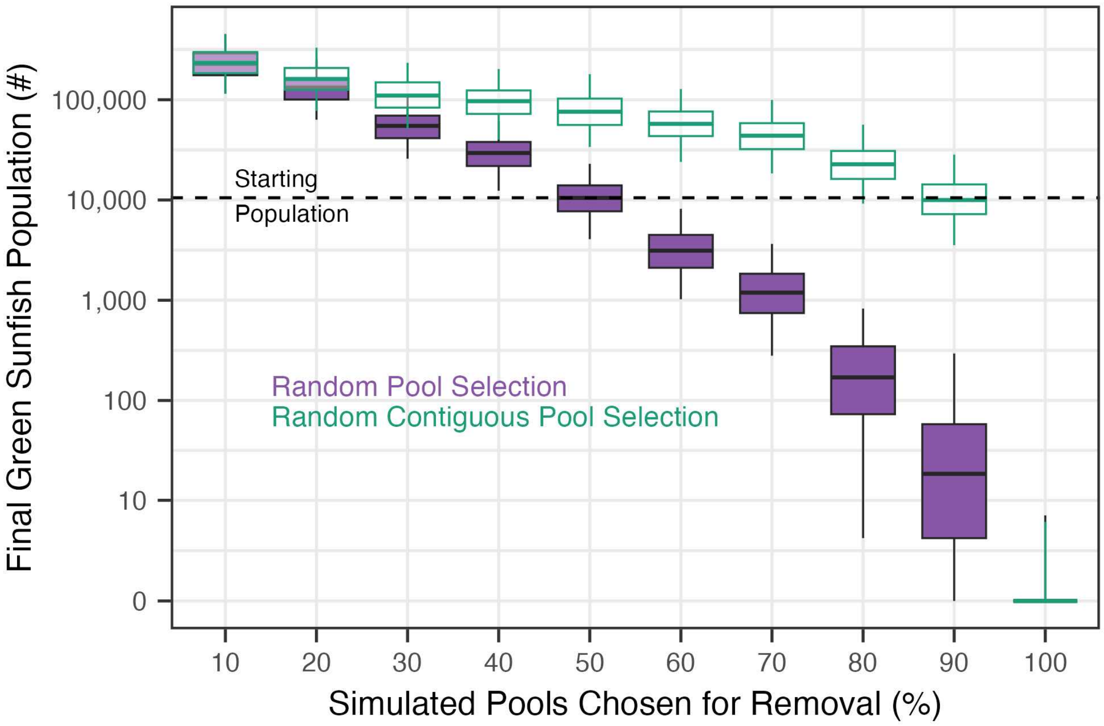

Figure 3.5: Simulated green sunfish population in McGee Wash, AZ at the end of the simulated removal program with a subset of random sites (purple, filled) and random contiguous sites (green, empty) chosen during each removal event. Boxplots display 1st quartile, median, and 3rd quartile for the box, with 2.5th and 97.5th percentile whiskers.

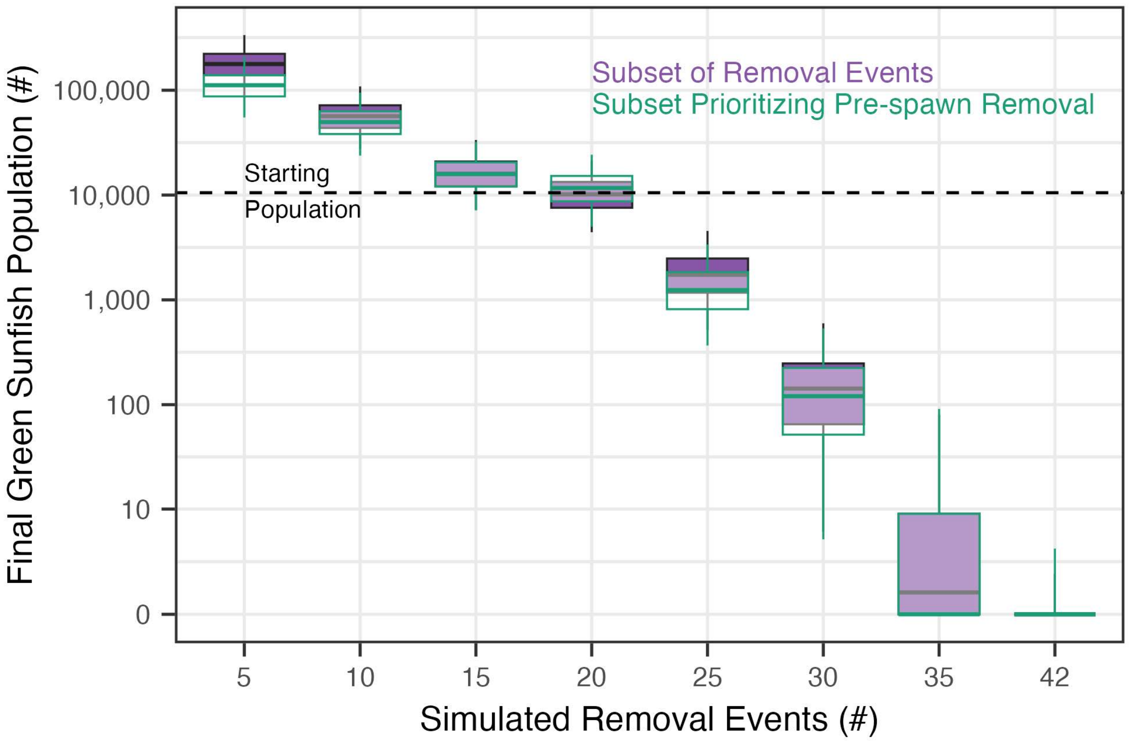

Figure 3.6: Simulated green sunfish population in McGee Wash, AZ at the end of the simulated removal program in strategies with a subset of evenly spaced removal events (purple, filled) and removal events chosen to prioritize pre-spawning (April of each year; green, empty). Boxplots display 1st quartile, median, and 3rd quartile for the box, with 2.5th and 97.5th percentile whiskers.

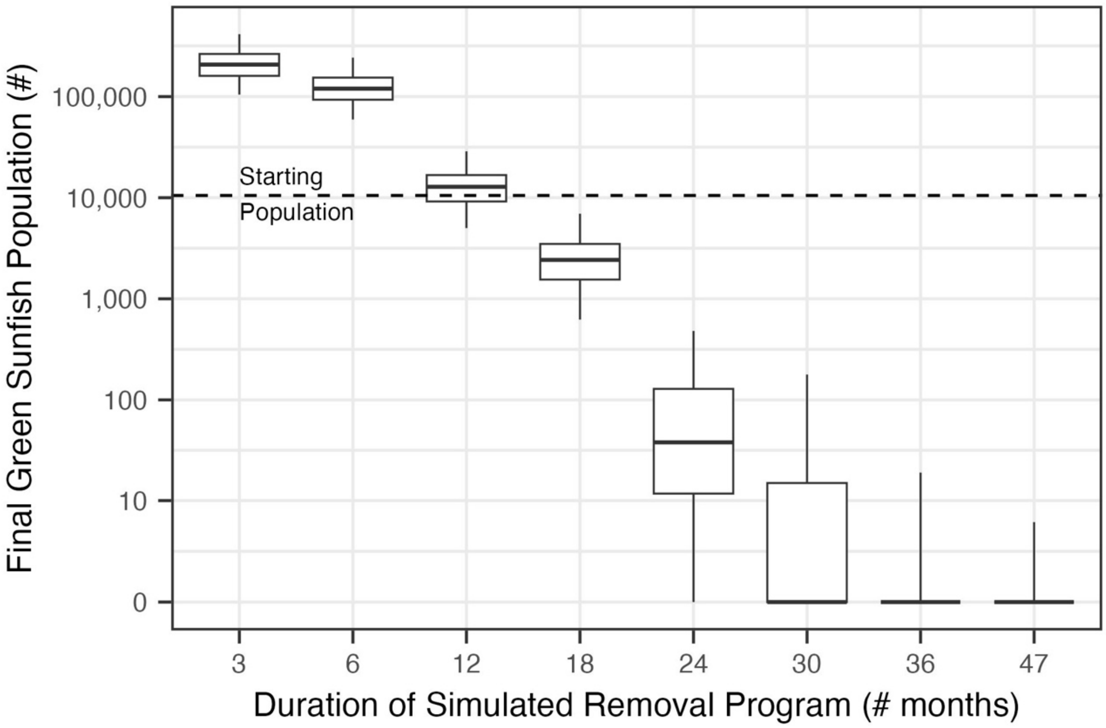

Figure 3.7: Simulated green sunfish population in McGee Wash, AZ at the end of the simulated removal program in strategies of different removal program durations. Boxplots display 1st quartile, median, and 3rd quartile for the box, with 2.5th and 97.5th percentile whiskers.

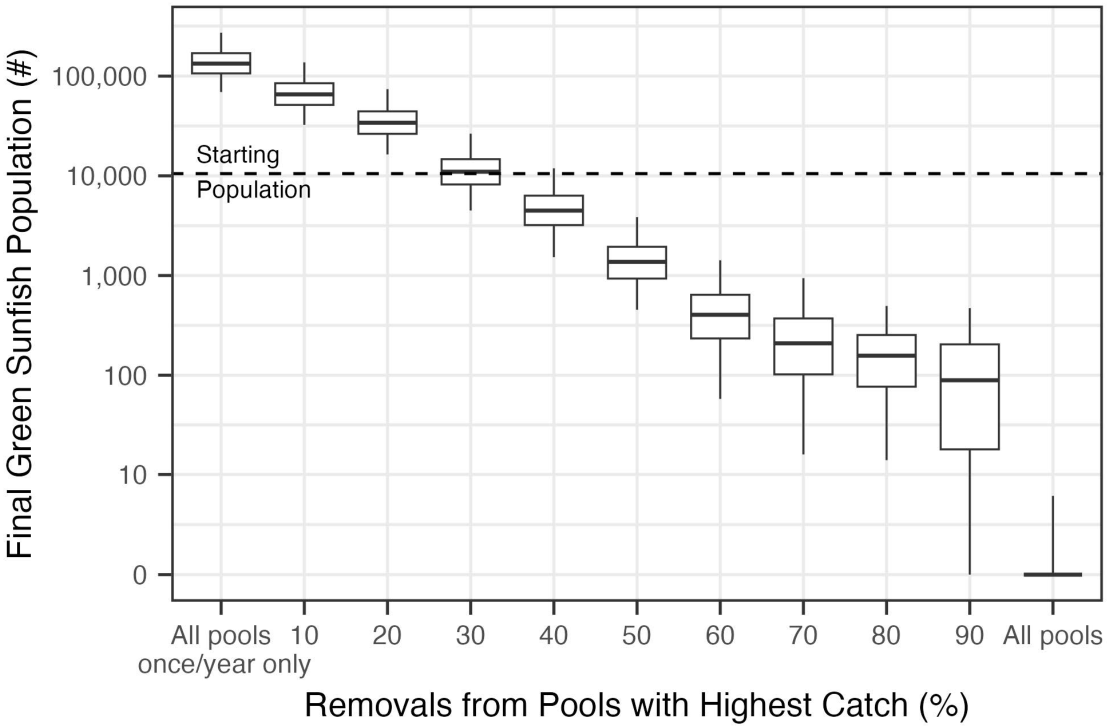

Figure 3.8: Simulated green sunfish population in McGee Wash, AZ at the end of the simulated removal program in strategies during which removals occurred in all sites once per year in August, then a percentage of the sites with the highest catch were continually visited until the following August. Boxplots display 1st quartile, median, and 3rd quartile for the box, with 2.5th and 97.5th percentile whiskers.

3.10 APPENDIX 3

Table A3.1: Mean and standard deviation for posterior distributions and assumed parameters for prior distributions in a Bayesian hierarchical model for green sunfish removal programs in McGee Wash and East Ash Creek, AZ.

Location	**Parameter**	**Mean**	**Standard Deviation**	**Prior Distribution**
McGee Wash	α – seine net	-1.24	0.0240	Uniform (-10, 10)
	α – hoop net and minnow trap	-2.80	0.0404	Uniform (-10, 10)
	α – backpack electrofisher	-1.86	0.0239	Uniform (-10, 10)
	β	0.00710	0.00693	Uniform (0, 10)
	s_1	0.998	0.000226	Uniform (0, 1)
	s_2	0.998	0.000346	Uniform (0, 1)
	f_{2018}	19.3	1.24	Normal (0, 12) T(0,)
	f_{2019}	0.487	0.704	Normal (0, 12) T(0,)
	f_{2020}	16.2	4.88	Normal (0, 12) T(0,)
	f_{2021}	9.27	7.08	Normal (0, 12) T(0,)
East Ash Creek	α – hoop net and minnow trap[1]	-2.54	0.0360	Normal (-2.80, 0.0404)
	α – backpack electrofisher[1]	-1.91	0.0221	Normal (-1.86, 0.0239)
	β	0.0684	0.0414	Uniform (0, 10)
	s_1[1]	0.998	0.000210	Normal (0.998, 0.000226)
	s_2[1]	0.997	0.000325	Normal (0.998, 0.000346)
	f_{2014}	0.312	0.184	Normal (0, 12) T(0,)

[1] Parameter prior distribution based on McGee Wash posterior distribution.

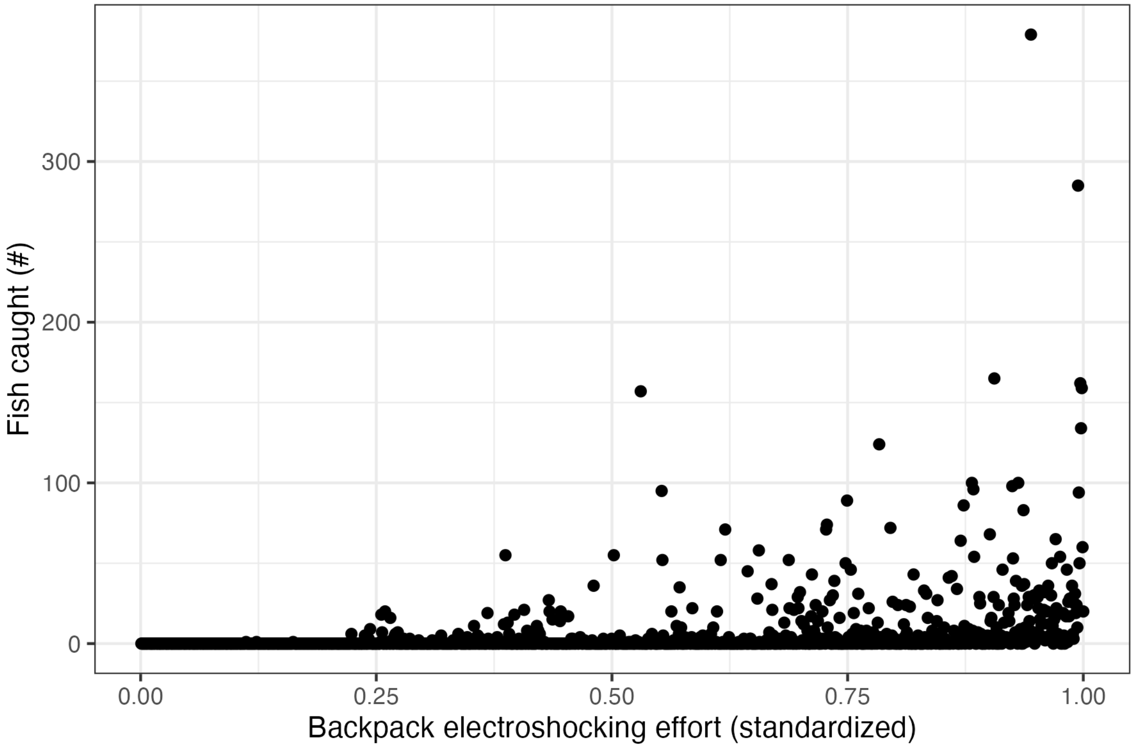

Figure A3.1: The standardized effort used in backpack electroshocking to capture green sunfish vs the harvest rate (the number of fish removed divided by the estimated abundance during each removal event and each pool) in McGee Wash, AZ. The effort was standardized from 0 to 1.

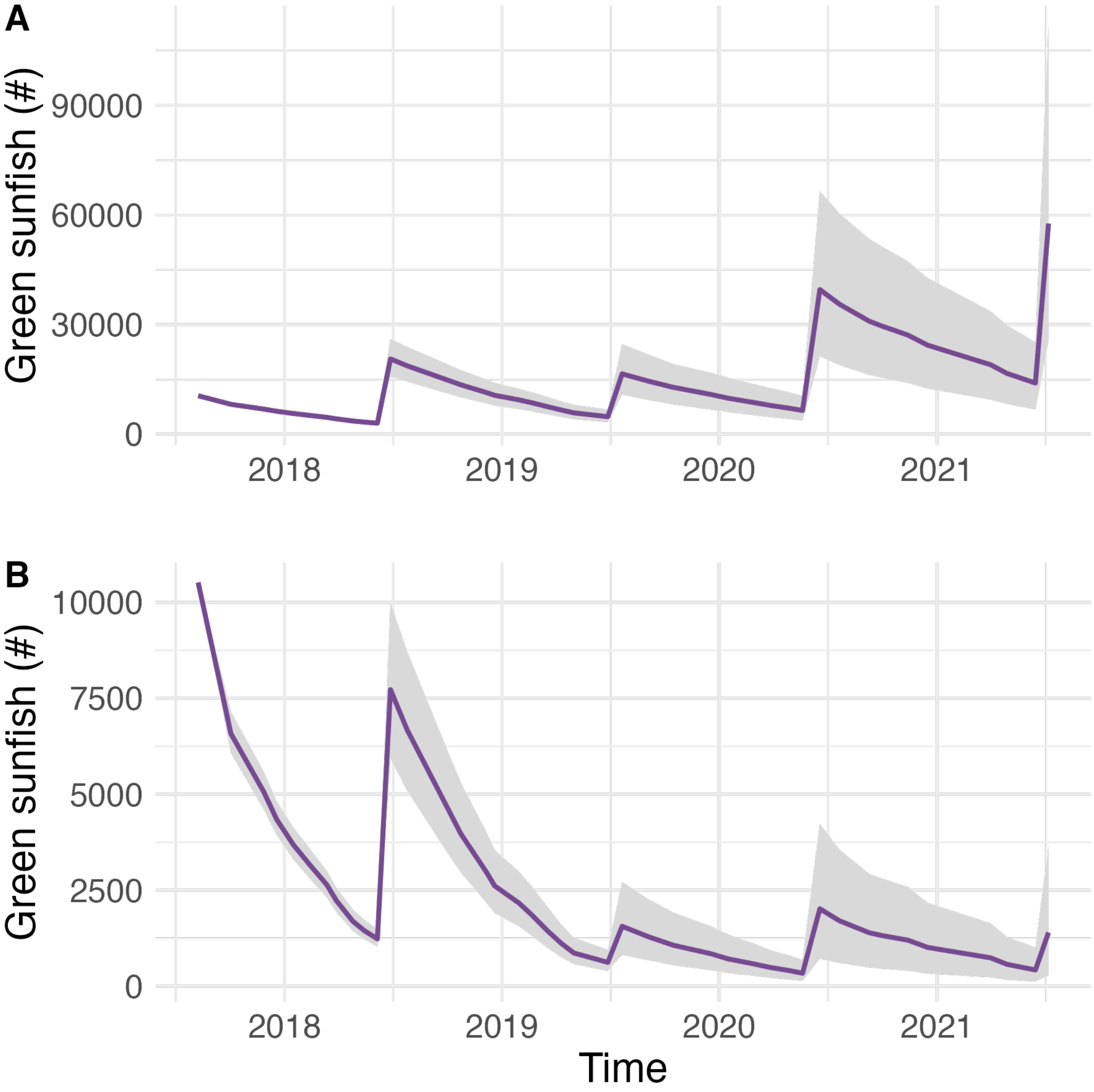

Figure 3.2: Simulated green sunfish populations (n=1000) in McGee Wash, AZ for strategies in which a 40% (panel A) and 80% (panel B) subset of random sites were chosen during each removal event. Grey ribbon represents the 95% confidence interval.

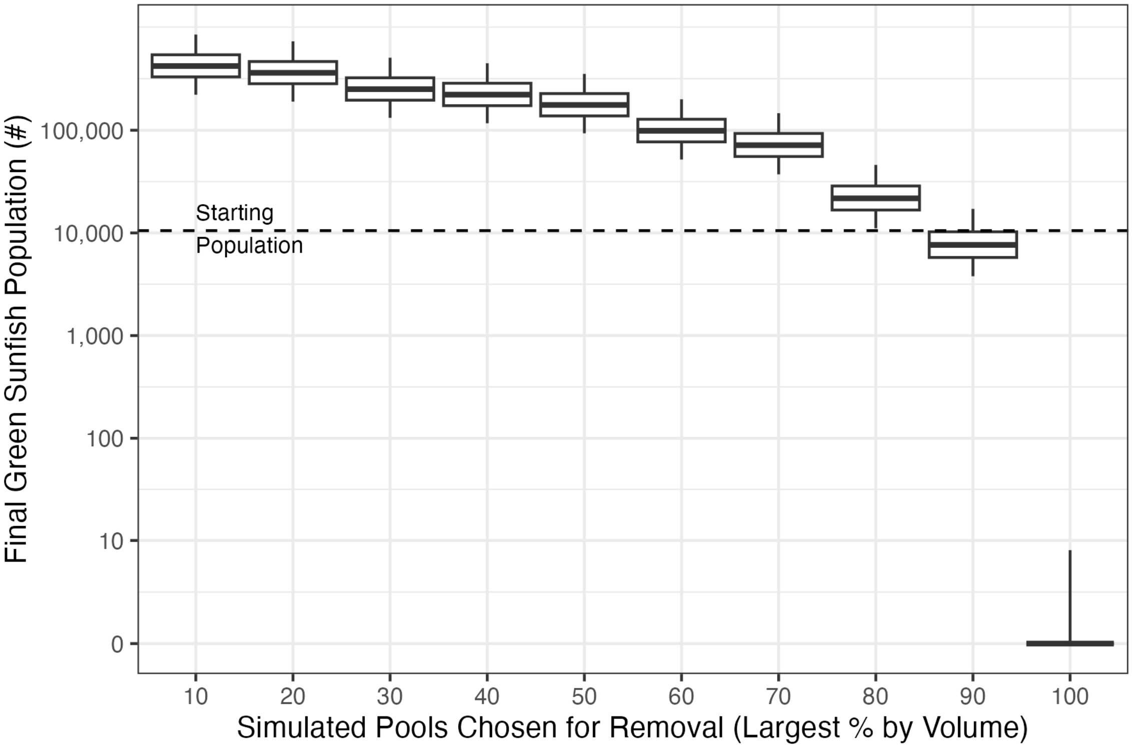

Figure A3.3: Simulated green sunfish population in McGee Wash, AZ at the end of the simulated removal program with a subset of sites chosen for removal based on pool volume. Boxplots display 1st quartile, median, and 3rd quartile for the box, with 2.5th and 97.5th percentile whiskers.

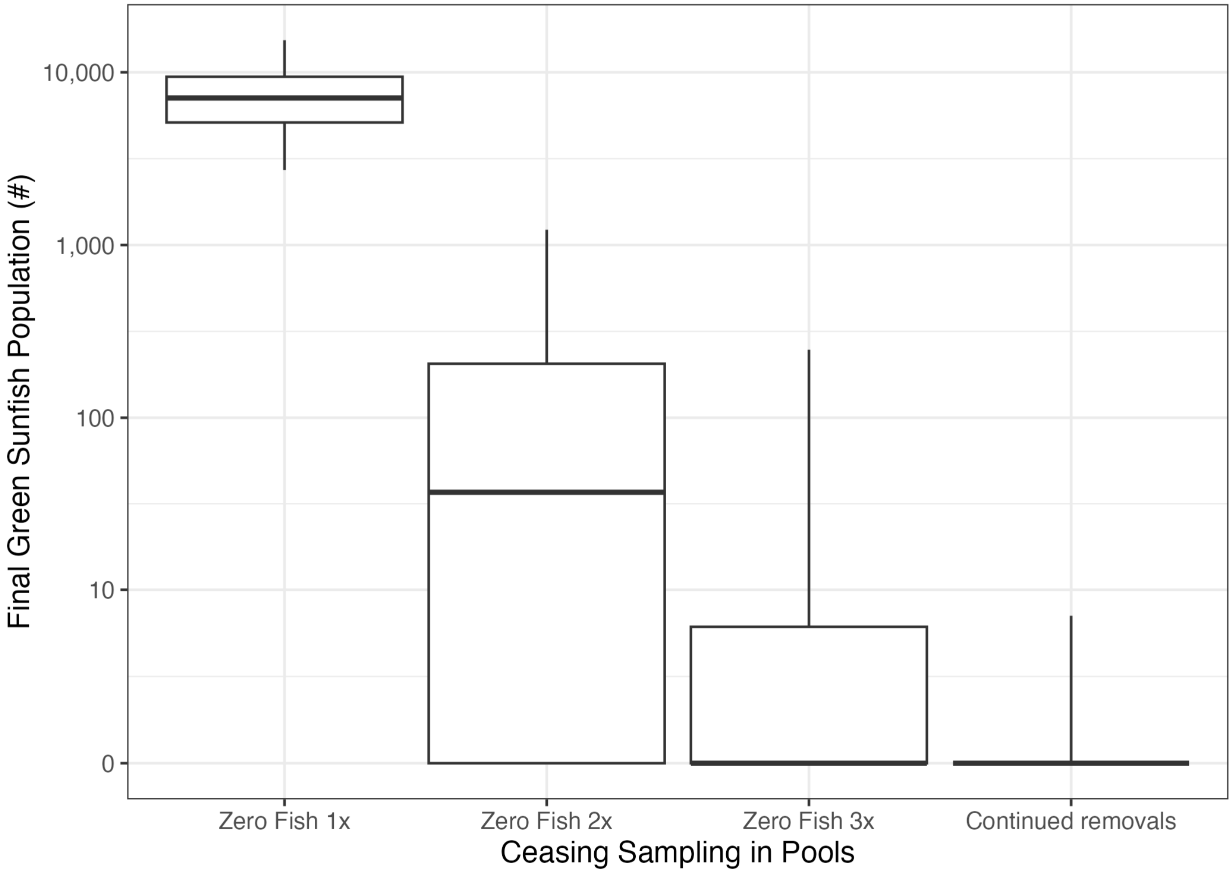

Figure A3.4: Simulated green sunfish population in McGee Wash, AZ at the end of the simulated removal program in strategies during which removals ceased in sites after zero fish were caught once, twice, or three times. Boxplots display 1st quartile, median, and 3rd quartile for the box, with 2.5th and 97.5th percentile whiskers.

Chapter 4. LEVERAGING PIT TAG DATA TO BETTER UNDERSTAND NORTHERN PIKEMINNOW MOVEMENT IN THE COLUMBIA RIVER BASIN

Publication history: This study was co-authored with Beth L. Sanderson, Katie A. Barnas, James R. Faulkner, Grant T. Waltz, Eric C. Winther, and Julian D. Olden. At the time that this dissertation was published, this chapter was in prep for publication.

4.1 ABSTRACT

Though native to the Columbia River Basin, northern pikeminnow have been the subject of long-term population control. This began in response to their increased predation of anadromous juvenile salmonids as a result of habitat modification due to hydropower dam construction. The Northern Pikeminnow Management Program (NPMP) is a targeted harvest program with a sport reward fishery that has been operating in the Columbia and Lower Snake Rivers since 1991. As a result of this sport reward fishery, over 5.7 million piscivorous (≥ 200mm FL) northern pikeminnow have been harvested for cash rewards. Each year, data are collected to monitor and evaluate the program; however, the program has come under scrutiny in recent years due to analytical methods that have not changed since the program's inception. Northern pikeminnow have been PIT tagged through the NPMP since 2003 to estimate the program's annual exploitation rate, with a goal of 10-20%, which feeds into an estimate of the program's annual reduction in predation. The model used to estimate the annual exploitation rate assumes closed populations separated by dams, an assumption that relies on limited evidence generated largely before PIT tag technology was deployed in the region. After being tagged, most northern pikeminnow are never recaptured, but PIT tag antennas passively track their movement. We combined data from the Columbia Basin PIT Tag Information System (PTAGIS) database with detailed NPMP tagging and harvest data to measure northern pikeminnow movement throughout the Columbia River Basin over two decades. Movement records reveal that individuals traveled at least as far as 968 km. Nearly 13% of northern pikeminnow tagged through the NPMP were detected in different river sections, separated by dams, from where they were initially tagged. Movement in tributaries and across mainstem dams reflects seasonal patterns aligned with

northern pikeminnow upstream spawning migration and outmigration of juvenile salmonids. Our increased understanding of northern pikeminnow movement informs calculation of the exploitation rate, one of the key measures of NPMP success. Further, as the NPMP evolves over time, information on northern pikeminnow movement may also contribute to future management strategies, like focusing removals on river reaches in which immigration outpaces emigration.

4.2 INTRODUCTION

Understanding fish movement is critical to effective fisheries management (Tilman and Kareiva 1997; Lucas and Baras 2001; Cooke et al. 2016). This knowledge provides necessary information for habitat protection, population estimation, and harvest implementation (Goethel, Quinn, and Cadrin 2011; Grüss et al. 2011; Herbst et al. 2017). Early work on freshwater fish movement gave rise to the “restricted-movement paradigm,” resulting from observations of sedentary adult stream fish (Gerking 1959). More recent studies have found that dispersal in freshwater fish species is leptokurtic, with frequent small-scale dispersal and relatively rare long-distance dispersal (Rodríguez 2002; Comte and Olden 2018b). The extent of movement in the stationary and mobile components, along with the share of each, vary by species and reflect different life-history strategies (Radinger and Wolter 2014; Comte and Olden 2018a). Timing, speed, and movement distance are influenced by both internal factors (e.g., hunger, endocrine state) and external factors (e.g., competition for food or space; Cooke et al. 2022), and long-distance migrations are often seasonal (Lucas and Baras 2001; Brönmark et al. 2014; Quinn 2018). Movement for the purpose of spawning or dispersal to suitable habitat may be critical to sustaining a viable population and have evolutionary implications (Rasmussen and Belk 2017). These movement patterns, including emigration and immigration, affect population dynamics, which in turn affect species interactions (e.g., competition, predation). Whether for species conservation or population suppression, effective management of fishes depends on knowledge of where and when species reside or migrate (Barton et al. 2015; Allen and Singh 2016; Cooke et al. 2016).

The construction of hydropower dams has resulted in significant impacts to freshwater fishes worldwide due to the blockage of longitudinal migration, loss of lotic habitat, and modification of environmental cues (Baras and Lucas 2001; Geist 2021; He et al. 2024). Over the past century, the construction of large hydropower dams in the Columbia River Basin (CRB) has restricted the movement of many fish species and altered species interactions (Beamesderfer, Ward, and Nigro 1996; Williams et al. 2005; Keefer et al. 2013). The decline of Pacific salmon and steelhead in the CRB has led to 12 runs becoming listed under the Endangered Species Act and over $400 million spent annually on salmonid recovery (Ruckelshaus et al. 2002; Williams et al. 2005; Jaeger and Scheuerell 2023). Dams have modified the flowing mainstem into a series of reservoirs with slow backwaters and warmer temperatures, which increases the amount of time juvenile salmonids are at risk of being consumed by predators during outmigration (Poe and Rieman 1988; Beamesderfer, Rieman, and Bledsoe 1990). Predation has recently been confirmed as a primary ecological threat to interior Columbia River Basin salmon and steelhead fisheries ("Rebuilding Interior Columbia Basin Salmon and Steelhead" 2022). One such predator, the northern pikeminnow (*Ptychocheilus oregonensis*), is native to the CRB, but its impacts on juvenile salmonids have substantially increased with the creation of reservoir habitat behind large dams (Beamesderfer, Ward, and Nigro 1996; Carey et al. 2012).

The Northern Pikeminnow Management Program (NPMP) was created in 1991 in response to research identifying northern pikeminnow as a significant predator of juvenile salmonids in the Columbia and lower Snake Rivers (Poe and Rieman 1988; Rieman et al. 1991). Initial studies estimated that large northern pikeminnow were consuming 16 million smolts annually, approximately 8% of the outmigrating population (Beamesderfer et al., 1996). The goal of the NPMP is to reduce predation on juvenile salmonids by shifting the size distribution of northern pikeminnow to smaller individuals that consume fewer fish by harvesting 10-20% of predatory sized fish (Winther, Waltz, and Martin 2024). Funding for the NPMP comes from the Bonneville Power Administration and it is co-coordinated by the Pacific States Marine Fisheries Commission, the Oregon Department of Fish and Wildlife (ODFW), and the Washington Department of Fish and Wildlife (WDFW). The program is primarily a sport reward fishery incentivizing northern pikeminnow harvest by recreational anglers in the Columbia River downstream of Priest Rapids Dam and in the Snake River downstream of Hells Canyon Dam. Anglers are rewarded with $6-$10 per qualifying northern pikeminnow, in a tiered system based on the cumulative number of fish harvested. The NPMP also includes a relatively small dam angling fishery conducted by the WDFW in the tailraces of the John Day and The Dalles dams. Over the past 33 years, this program has spent $35 million on tiered bounty reward payments for the harvest of over 5.7 million northern pikeminnow ≥ 200mm fork length (Winther, Waltz, and Martin 2024).

The NPMP has been heralded as successful over the past three decades, though recent reviews have challenged the program's key assumptions (Cramer et al. 2012; Fausch et al. 2019). The primary success metric of the NPMP is the exploitation rate, calculated separately for each river reach (i.e., between mainstem dams) via mark-recovery techniques using either external or passive integrated transponder (PIT) tags. The exploitation rate of each river reach (u_j) is calculated using the Peterson estimator (Ricker 1975) as $u_j = R_j / M_j$, where R_j is the number of tagged fish recaptured during the season in river reach j and M_j is the number of fish tagged in river reach j (Waltz et al. 2022). The annual goal of a 10-20% exploitation rate has been accomplished in most years (Waltz et al. 2024) and was initially predicted to reduce northern pikeminnow predation on juvenile salmonids by up to 50% (Rieman and Beamesderfer 1990). However, many of the assumptions made, and rapid assessment methods used, at the program's onset have not been re-examined since the 1990s (Fausch et al. 2019; Gregory 2020). The CRB food web has also changed substantially since that time, including the increase in abundance and distribution of nonnative smallmouth bass (*Micropterus dolomieu*) and walleye (*Sander vitreus*), additional predators of juvenile salmonids (Carey et al. 2011; Rubenson and Olden 2020; Waltz et al. 2024). Central to program evaluation is the assumption of closed systems, with northern pikeminnow movement restricted by mainstem dams. Previous research on northern pikeminnow movement is limited, though individuals have been observed traversing The Dalles Dam via short-range radio tags (Martinelli and Shively 1997).

The degree of northern pikeminnow movement may compromise the success of the NPMP in reducing predation on juvenile salmonids. First and foremost, the current assumption of closed systems with no movement between river reaches separated by dams does not account for immigration from other populations that may compensate for removal efforts. Second, the estimated reach-specific exploitation rate may be over- or under-estimated if fish are disproportionately moving between river reaches. As part of the NPMP, the ODFW has conducted fisheries-independent monitoring to track relevant metrics (e.g., abundance index) to account for unknowns regarding northern pikeminnow population dynamics (Friesen and Ward 1999; Waltz et al. 2024). While these indices help to inform managers of potential changes in predatory fish dynamics in the CRB, the NPMP would benefit from additional information on northern pikeminnow life history, including movement patterns. Increased knowledge of northern pikeminnow movement can be used to improve the accuracy of both the exploitation rate and the reduction in predation estimates. PIT tags have been used to calculate the NPMP exploitation rate since 2003. The number of tagged fish that are recovered through the sport reward fishery is an integral component of the program's annual exploitation rate calculation. PIT-tagged fish captured through the sport reward fishery are worth considerably more money ($200), incentivizing fish submission, and all harvested fish are scanned for a PIT tag when turned in at a registration station. PIT tag antennas have also been passively collecting movement data for over 20 years as tagged northern pikeminnow move throughout CRB, and these detections are logged in the online PIT Tag Information System (PTAGIS) database. The combination of recovery and detection data provide a multidecade source of northern pikeminnow movement records throughout the CRB.

We aimed to utilize the PIT tag records of northern pikeminnow tagged through the NPMP to ask: Are northern pikeminnow moving across dams, thereby violating the assumption of no movement between river reaches? And if so, are they moving between river reaches disproportionately, leading to bias in the exploitation rate estimations? To answer these questions, we first determined how far northern pikeminnow are detected moving within the CRB and for how long after tagging. We subsequently investigated how many northern pikeminnow were detected crossing over mainstem dams into different river reaches of the NPMP harvest area. We leveraged existing northern pikeminnow PIT tag data collected from ODFW, WDFW, and PTAGIS databases between 2003-2022. This investigation provides an opportunity to understand better northern pikeminnow movement patterns for the refined management of these native predators of ESA listed salmon and steelhead.

4.3 METHODS

We accessed northern pikeminnow PIT tag data between 2003-2022 from the ODFW, the WDFW, and the PTAGIS databases. The four broad categories of northern pikeminnow PIT tag data included tagging, recaptures, passive detections, and mortalities. Only northern pikeminnow tagged through the NPMP were included in our analyses (i.e., northern pikeminnow tagging studies conducted for other purposes were not included). Each year, between early April and mid-June, ODFW tagged between 400 and 2500 northern pikeminnow ≥ 200mm fork length.

Tagging was conducted along shallow shoreline areas between river kilometer (rkm) 76 to rkm 637 in the mainstem Columbia River and between the Little Goose Dam to rkm 251 in the mainstem Snake River. Fish were captured via boat electrofishing and 134.2 MHz PIT tags were injected into the dorsal sinus cavity (Waltz et al. 2024). Previously tagged northern pikeminnow that were recaptured by the ODFW during the tagging process were recorded as recaptures, measured for length, and released back to the river alive. Passive detections of the northern pikeminnow PIT tags were recorded within the PTAGIS database by antennas throughout the CRB (Fig. 4.1). These antennas were installed in adult fish passage and juvenile bypass facilities present at many mainstem and tributary dams. Instream PIT tag arrays captured northern pikeminnow detections throughout the CRB. A trawl net outfitted with PIT tag antennas and deployed in the Columbia River estuary also detected several northern pikeminnow. Mortality records came from the sport reward fishery harvests, dam angling fishery harvests, and a single mortality reported during tagging efforts. When northern pikeminnow were submitted via the sport reward fishery, each fish was checked for a PIT tag in a standardized method using an angled tube outfitted with a PIT tag scanner.

Collection records included latitude and longitude, with the exception of sport reward fishery harvests, for which we used the river kilometer recorded by ODFW for tagging and recaptures. Instream array and dam passage facility location data are available on the PTAGIS website. Anglers who participate in the sport reward fishery report only the NPMP Location (numbered 1 through 12) in which they captured the fish, not the precise capture location (Hone et al. 2024). Therefore, mortalities through the sport reward fishery were assigned harvest locations that are the rkm midpoint of each of these twelve NPMP Locations. Each fish detection was assigned to one of nine river reaches separated by mainstem dams used by the ODFW to calculate area-specific exploitation rate (1: The Columbia River below Bonneville Dam, 2: between Bonneville and The Dalles Dams, 3: between The Dalles and John Day Dams, 4: between John Day and McNary Dams, 5: between McNary and Priest Rapids Dam on the Columbia River plus the Snake River between the confluence with the Columbia River and Ice Harbor Dam, 6: The Snake River between Ice Harbor and Lower Monumental Dams, 7: between Lower Monumental and Little Goose Dams, 8: between Little Goose and Lower Granite Dams, and 9: between Lower Granite and Hells Canyon Dams).

Processing of raw passive detection data involved consolidating repetitive detections and assigning dam passage in adult fishways. When multiple detections for an individual fish were logged at a single site within 24 hours, these detections were consolidated into a single data point based on the earliest time. Passage through adult fishways, either upstream or downstream, was conservatively assigned using a series of decision rules unique to each facility. Based on the antenna array diagrams available through PTAGIS, we assumed individual fish started upstream of the dam if their first detection was at the furthest upstream antenna at that dam. Otherwise, they were classified as entering the fish passage facility downstream of the dam. Fish were supposed to have traveled through the adult fishway based on their last detection. If an individual started downstream of the dam and their last detection was at the most upstream antenna, they were assumed to have passed through the fish ladder. If not, we classified the fish as remaining downstream of the dam. For individuals that started upstream, we only marked them as passing downstream if the last detection was at the furthest downstream antenna. Many adult fish passage facilities contain a series of weirs with antennas that are unable to detect every time a PIT tagged northern pikeminnow moves past an antenna. Fish may enter an adult fishway from upstream or downstream without necessarily passing all the way through, whereas juvenile bypass facilities only allow downstream passage.

We measured distance traveled by individual northern pikeminnow between detections along the one-dimensional river network. CRB network data were sourced from the National Hydrography Dataset (U.S. Geological Survey 2018). The “riverdist” package was used to calculate distance and time between detections (Tyers 2024). All analyses were performed in R version 4.4.0 (R Core Team 2024). Fish that traveled into tributaries were classified as remaining within the same river reach as the mainstem from which they traveled. When fish were detected traveling through the Priest Rapids Dam adult fishway, outside of the NPMP scope, they were considered in the same river reach as downstream of the Priest Rapids Dam. No northern pikeminnow tagged through the NPMP were detected further upstream in the Columbia River than the Priest Rapids Dam adult fishway. Detection probability was calculated for each mainstem dam in the upstream and downstream directions as the number of detected movement events across a particular dam divided by the total number of movement events (detected and undetected). Undetected movement across a particular mainstem dam is determined by a detection event on the other side of the dam, implying movement across the dam.

4.4 RESULTS

A total of 22,295 northern pikeminnow during the period 2003-2022 were tagged by the ODFW as part of the NPMP. Of that total, 5,967 fish had subsequent detections and were included in our analyses (Fig. 4.1). Most of these fish were detected only once (n=5,178), with decreasing numbers of fish detected multiple times (313 fish detected twice, 145 fish detected three times), up to 76 fish with over 10 detections each. The majority of detections were mortalities (sport reward fishery: n=4,859, dam angling fishery: n=140, other: 1), followed by dam passage facilities at 16 dams (adult fishway: n=1,896 and juvenile bypass: n=134), instream remote detections at 38 sites (n=1,503), recaptures (n=304), and trawl net detections (n=4).

Northern pikeminnow were detected traveling a median of 32km after PIT tag implantation (Fig. 4.2). A wide range of distances were observed, with a distribution skewed to the right in which the 10th percentile was 5km and the 90th percentile was 107km. The furthest distance traveled was 968km by an individual northern pikeminnow over a 6-year period (2014-2019), tagged above the Lower Granite Dam and detected 11 times at multiple instream remote arrays within the Grande Ronde River and its tributaries (Box 4.1). The sport reward fishery data were the only detection type that did not include precise location data. When the sport reward fishery detections were excluded, we observed a similar median with greater spread (31km, 10th percentile: 1km, 90th percentile: 180km). The time between initial tagging and last detection record of each PIT tag ranged from 0-18.2 years (10th percentile: 0.09 years; 90th percentile: 4.33 years) with a median of 1.2 years, or 423 days (Fig. 4.2).

Of the tagged northern pikeminnow with subsequent detections, 12.8% were detected traveling across a dam into a different river reach (Fig. 4.3). Nearly all of these movements were to adjacent reaches (12.1%), with only 0.7% of tagged fish detected traveling farther. The percentage of tagged fish that were detected leaving their tagged reach varied from 2 to 31% across reaches (Table 4.1). The number of fish tagged in each reach also varied; from 0 between the Lower Monumental and Little Goose Dams, to 9,187 (41% of all tagged fish) downstream of the Bonneville Dam. The percentage of tagged fish from each reach with subsequent detections was broadly representative of the percentage of fish that were tagged in each reach (Table 4.1). Movement detected into and out of river reaches 2 and 3 was disproportionate (Fig. 4.3). In reach

2, between the Bonneville and The Dalles Dams, 195 northern pikeminnow were detected moving into the reach, and 425 were detected moving out of the reach (a loss of 230 tagged fish). In reach 3, between The Dalles and John Day Dams, 261 northern pikeminnow were detected moving into the reach, with 41 moving out of the reach (a gain of 220 tagged fish). The remaining reaches showed nearly even losses and gains of tagged fish (reach 1: +12 overall, reach 4: +4, reach 5: -2, reach 6: +3, reach 7: +11, reach 8: +9, reach 9: -19).

Detection probability was variable between mainstem dams, though much higher in the upstream, relative to downstream, direction (Table 4.2). All eight mainstem Columbia and Snake River dams within the NPMP spatial scope detected some, but not all, northern pikeminnow movement upstream. The Dalles, McNary, and Bonneville Dams had the highest upstream detection probability, ranging from 0.74 to 0.84. Detection of downstream movement was much lower for most dams.

Seasonal patterns of movement were evident in the subset of fish that were detected in tributaries and using hydropower adult fish passage facilities. Only 6% of tagged fish with subsequent detections were recorded traveling into a tributary of the Columbia or Snake Rivers via instream arrays or fish passage facilities. Within the detections in tributaries from arrays and dams operating year-round (29 sites, 326 fish, 1,287 detections), we found a seasonal peak from May-July and minimal detections from November-March (Fig. 4.4A). Tributaries with the highest numbers of detections were the Grande Ronde (711 detections; 138 fish), the Yakima (229 detections; 80 fish), and the Deschutes (224 detections; 63 fish). Seasonal patterns were also found in detections via several mainstem dam adult fish passage facilities with the highest number of detections representing passage upstream through the dam. The BO4 Bonneville Dam WA Ladder Slots adult fish passage records included 190 fish and 391 records of upstream movement with a seasonal peak from June-September (Fig. 4.4B). Just up river, The Dalles Dam East Fish Ladder (TD1) adult fish passage records included 232 fish and 365 detections with a peak from May-July, but especially high in June (Fig. 4.4C). Further upstream, the Priest Rapids Dam adult fish passage facility (PRA) included records of 42 fish and 110 detections showing a peak in September-October (Fig 4.4D).

4.5 DISCUSSION

Northern pikeminnow were found to be moving further throughout the CRB than previously reported, with movement across dams and into tributaries. These results affirm previous studies demonstrating the utility of PIT tag arrays to capture location data across a large spatial scale for many years after tagging (Brodersen, Hansen, and Skov 2019). Previous studies using radio tags in northern pikeminnow achieved finer resolution movement information (Poe 1994; Martinelli and Shively 1997), though radio tags are limited by battery life. Because PIT tags are activated by antennas, they essentially last the lifetime of the fish (up to 18.2 years from our results). Spatial resolution, however, is dependent on the number and location of antennas throughout the basin. Our research is the only northern pikeminnow movement study in over 25 years, and the first to track northern pikeminnow movement in the CRB using PIT tags.

Northern pikeminnow movement patterns reported here reflect their life history, including seasonal foraging and spawning migrations. Increased detections in tributaries from May-June is consistent with spawning migrations upstream (Beamesderfer 1992). Adult northern pikeminnow travel upriver and into tributaries to broadcast spawn, dependent on temperatures reaching 14°C, which generally occurs between June and early July (Gadomski et al. 2001). The seasonal variation in dam passage upstream varied between dams. Northern pikeminnow movement upriver through The Dalles adult fishway peaked in June, whereas the Bonneville and Priest Rapids Dam adult fishways showed peaks later in the year. These patterns may be related to spawning or foraging. Previous research has attributed short-term movements near dam tailraces to foraging for juvenile salmonids during outmigration (Martinelli and Shively 1997). Movement between river reaches may be related to competitive interactions driving northern pikeminnow to disperse, or higher prey availability drawing them in. Greater knowledge of northern pikeminnow movement has been made possible through the installation of arrays within the CRB, many of which were created to monitor Pacific salmonid survival and movement. Despite the highly altered habitat of the CRB, our results suggest that some northern pikeminnow movement patterns persist.

We revealed the minimum distance traveled by northern pikeminnow in the Columbia River Basin. Between PIT tag antenna detections, individual fish are engaged in shorter distance movement for dispersal, spawning, or foraging. The movement captured with PIT tags begins when the fish is tagged (at a minimum of 200mm), not tracking any movement before the fish reaches a length of at least 200mm. When recaptured or harvested through the NPMP, northern pikeminnow are scanned for the presence of a PIT tag, with high detection probability. However, dam passage and instream remote detection antennas have unknown detection probabilities for northern pikeminnow. We found a range of detection probabilities for movement across dams, upstream and downstream, mainly reflecting the structural and antenna design differences at each dam passage facility. The PIT tag is placed in the dorsal sinus cavity of northern pikeminnow (Waltz et al. 2024). However, it is placed in the peritoneal cavity in salmonids (Cook et al. 2014), and many of the PIT tag antennas throughout the CRB were initially installed to monitor the movement and behavior of anadromous salmonids. Detection probability is also impacted by fish length (Saboret, Dermond, and Brodersen 2021), species (Cucherousset et al. 2010; Kelly et al. 2017) and instream conditions. Seasonal increases in stream velocity may decrease detection probability of instream arrays (Cucherousset et al. 2010; O'Donnell, Horton, and Letcher 2010). In addition, during high flooding, fish may be outside of the detection range (Linnansaari et al. 2007), even if the array is operating year-round.

Northern pikeminnow move across mainstem dams of the CRB into different mainstem river reaches. Our results suggest that the number and proportion of northern pikeminnow that move across dams are disproportionate between river reaches, though we cannot directly compare these proportions or measure bias in exploitation rate estimates. We were able to detect movement across dams using fish passage facilities in many cases. However, northern pikeminnow may go undetected traveling through dams due to imperfect detection, especially in the downstream direction in which they may pass over dam spillways or through turbines where there are no tag detectors. Indeed, detection probabilities were lower for downstream movement events at most mainstem dams. In addition to dam passage antennas, the records of harvest, recaptures, and instream arrays revealed movement across dams simply by detecting an individual up or down river of their tagged river reach. Therefore, the ability to detect movement across dams is dependent in part on the distribution of PIT tag arrays within the watershed. Within the CRB, PIT tag arrays have been installed unequally across basins and at different times in history. In addition, the ability to detect northern pikeminnow via harvest through the sport reward fishery is highly variable because it is dependent on angler effort, the number of fish tagged in each reach, and the size of each reach, all of which vary greatly (Winther, Waltz, and Martin 2024). Due to these limitations, our results cannot directly compare movement between reaches, but this may be possible by incorporating additional data or using a hidden Markov model to estimate movement probabilities.

Though northern pikeminnow are a highly managed species in the CRB, most research on their movement and life history was conducted over 25 years ago, leaving many unknowns (Rieman and Beamesderfer 1990; Poe 1994; Martinelli and Shively 1997). Fish movement is complex and dependent on a number of internal and external factors, including ontogenetic dietary shifts, interspecific competition for food and space, and human-created barriers to movement (Sánchez-Hernández et al. 2019; Cooke et al. 2022; He et al. 2024). Northern pikeminnow become piscivorous above 230mm (Beamesderfer et al., 1996; Vigg et al., 1991), and this dietary shift is likely driving movement patterns with respect to foraging. However, the introduction of nonnative prey such as American shad (*Alosa sapidissima*) and Siberian prawn (*Palaemon modestus*) may be playing a larger role in northern pikeminnow diets than their native prey, depending on the season (Erhardt and Tiffan 2016; Quinn et al. 2024; Waltz et al. 2024). As nonnative piscivorous fish, including smallmouth bass and walleye, increase in the CRB over time (Rubenson and Olden 2020; Waltz et al. 2024), competition may contribute to northern pikeminnow dispersal. All northern pikeminnow detected in the tributaries as part of this study were initially tagged in the mainstem, indicating some movement from the mainstem to tributaries. It is unknown, however, if distinct tributary populations of northern pikeminnow exist, and if so, whether they tend to remain in upstream tributaries, out of the reach of NPMP harvest. Although it is challenging to manage northern pikeminnow and other fishes within the large spatial scope of the CRB with limited data and research funding, effective management relies on accurate data about the system.

Our research offers insight into the movement of northern pikeminnow, with implications for current management. Through 2022, the NPMP employed a capture-recovery model to estimate the exploitation rate of northern pikeminnow, a key metric of program success, based on the number of tagged fish that are harvested in each river reach (Waltz et al. 2022). This model assumes closed systems with no movement across dams. However, our analysis revealed that 12.8% of tagged northern pikeminnow were detected traveling across mainstem dams, with disproportionate movement between some river reaches. These results suggest that some reach-specific exploitation rates may be biased, leading to over- or under-estimation, though additional research is needed. In more recent years, the ODFW has explored the use of a systemwide mark-recovery exploitation model to replace the reservoir-specific exploitation model (Waltz et al. 2024). Conversely, over 87% of northern pikeminnow were only detected in the reach in which they were tagged. This suggests that reaches with high exploitation may not be recolonized quickly, and intensive harvest could have substantial temporary impacts on northern pikeminnow populations. Therefore, reaches with high northern pikeminnow populations or consumption rates could be more heavily targeted for harvest, with greater impacts to juvenile salmonids. As the NPMP evolves and the ecology of the CRB continues to shift, the movement of northern pikeminnow is an essential consideration in managing their populations for the conservation of Pacific salmon and steelhead.

4.6 ACKNOWLEDGMENTS

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4.8 TABLES

Table 4.1: Differences in northern pikeminnow tagging and inter-reach detection in each river reach of the Northern Pikeminnow Management Program from 2003-2022. Number and percentage of tagged northern pikeminnow by reach, those tagged with subsequent detections by reach, and those detected leaving their tagged reach.

River Reach[a]	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Number (%) of total tagged fish from each river reach (total: 22,227)	9,187 (41)	3,960 (18)	905 (4)	532 (2)	4,197 (19)	91 (0.4)	0 (0)	1,336 (6)	2,019 (9)
Number (%) of tagged fish with subsequent detections from each river reach (total: 5,967)	2,373 (40)	1,415 (24)	247 (4)	73 (1)	953 (16)	23 (0.4)	0 (0)	337 (6)	546 (9)
Number (%) of tagged fish detected leaving tagging reach (total: reach-dependent)	156 (7)	425 (30)	41 (17)	15 (21)	16 (2)	4 (17)	- (-)	28 (8)	37 (7)

[a] River reaches defined as 1: The Columbia River below Bonneville Dam, 2: between Bonneville and The Dalles Dams, 3: between The Dalles and John Day Dams, 4: between John Day and McNary Dams, 5: between McNary and Priest Rapids Dam on the Columbia River plus the Snake River between the confluence with the Columbia River and Ice Harbor Dam, 6: The Snake River between Ice Harbor and Lower Monumental Dams, 7 : between Lower Monumental and Little Goose Dams, 8: between Little Goose and Lower Granite Dams, and 9: between Lower Granite and Hells Canyon Dams.

Table 4.2: Movement across dams by northern pikeminnow tagged through the Northern Pikeminnow Management Program from 2003-2022, separated by upstream/downstream and detected/undetected. Each number represents a single movement event between river reaches (individual fish may be represented more than once). Upstream and downstream detection probability is also displayed as the proportion of detected movements out of the total.

Mainstem Dams	Upstream, Detected	Upstream, Undetected	Upstream Detection Probability	Downstream, Detected	Downstream, Undetected	Downstream Detection Probability
Bonneville	459	165	0.74	117	419	0.22
The Dalles	368	69	0.84	0	216	0.00
John Day	8	9	0.47	0	10	0.00
McNary	33	7	0.83	3	26	0.10
Ice Harbor	9	8	0.53	0	10	0.00
Lower Monumental	2	6	0.25	1	2	0.33
Little Goose	9	15	0.38	10	11	0.48
Lower Granite	42	12	0.78	3	56	0.05

4.9 FIGURES

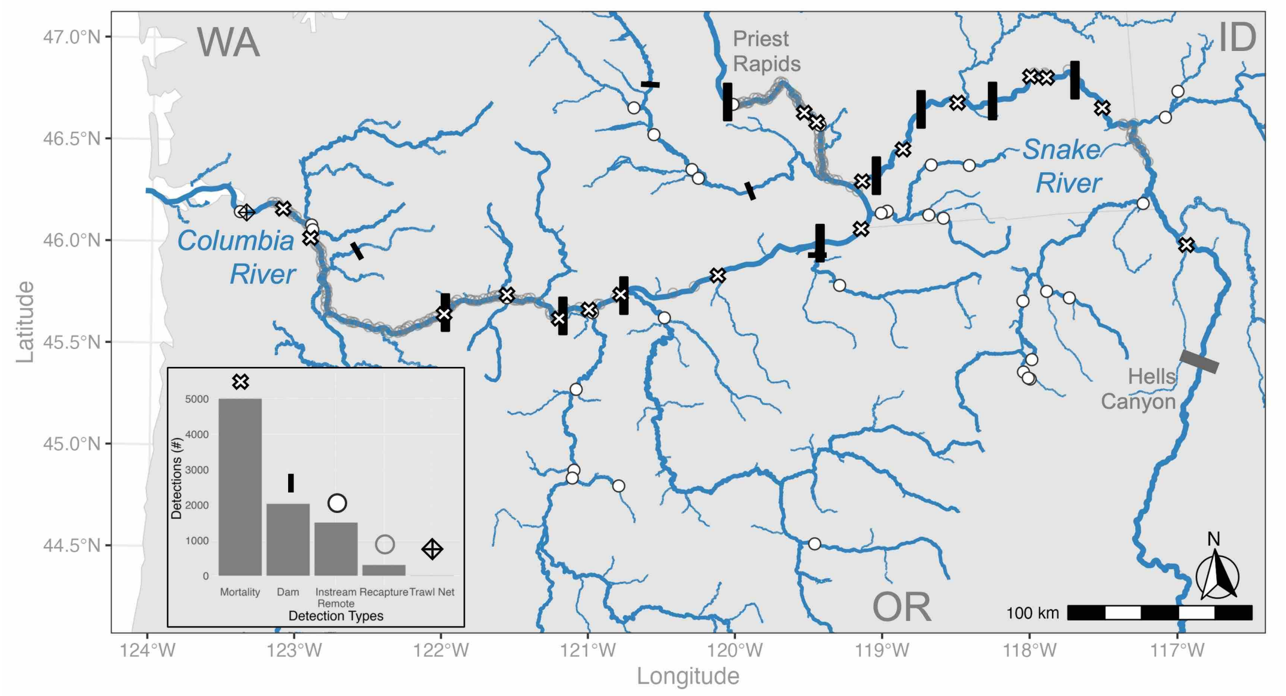


Figure 4.1: Map of the Columbia River Basin within the Northern Pikeminnow Management Program bounds: the mainstem Columbia River downstream of the Priest Rapids Dam and the mainstem Snake River downstream of Hells Canyon Dam. Lower left inset shows the number of detections after tagging for each detection type with the symbol representing each detection type on the map. Black rectangles represent dams with fish passage; the grey rectangle represents the Hells Canyon Dam, without fish passage.

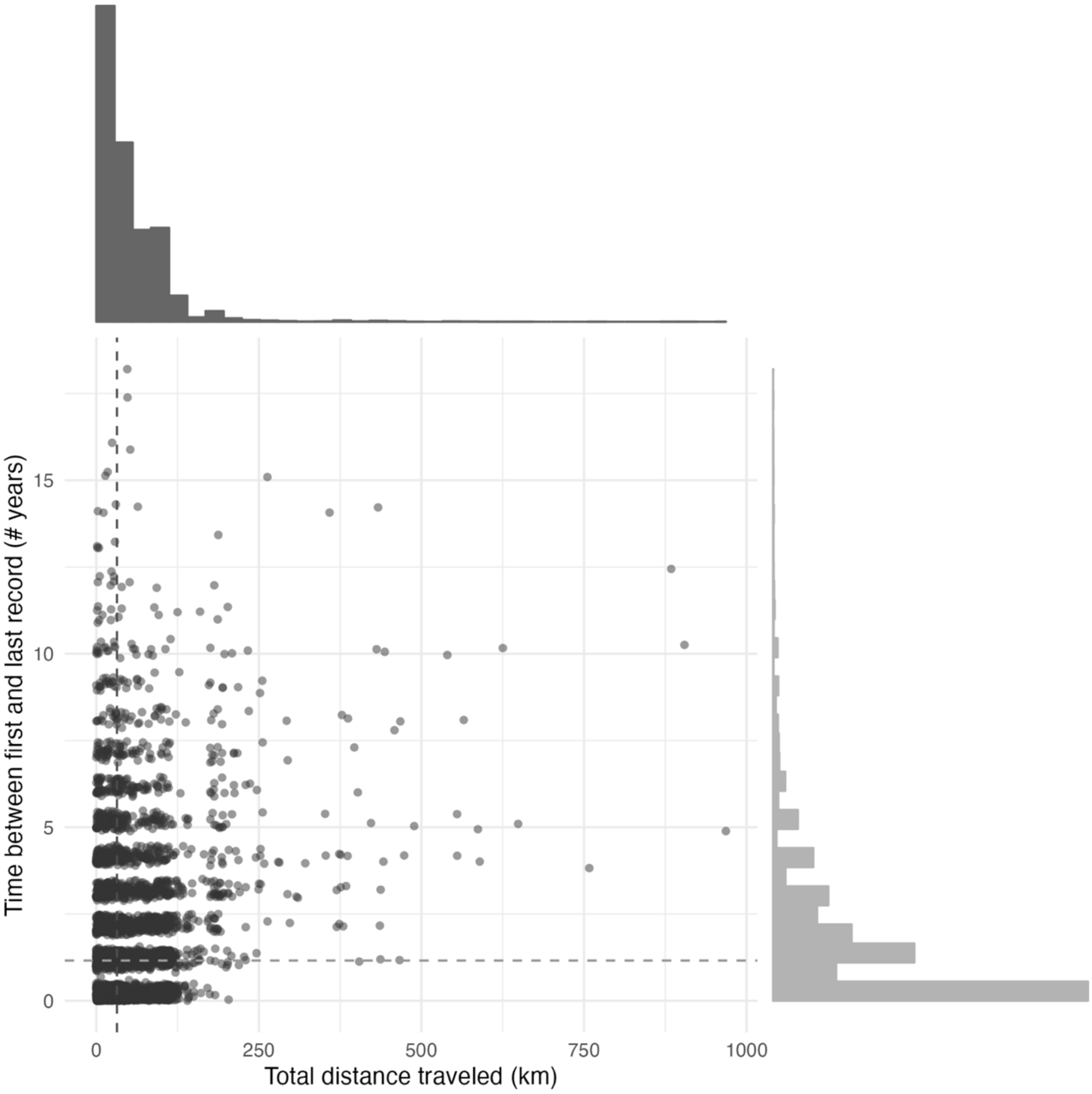


Figure 4.2: Scatterplot of the total distance traveled (km) vs. the time between first and last record (number of years) for northern pikeminnow PIT-tagged through the Northern Pikeminnow Management Program and subsequently detected within the Columbia River Basin. Marginal histograms are shown for total distance traveled (top) and time between first and last record (right). The vertical dashed line represents the median of total distance traveled (32 km) and the horizontal dashed line represents the median of time between first and last record (1.2 years, 423 days).

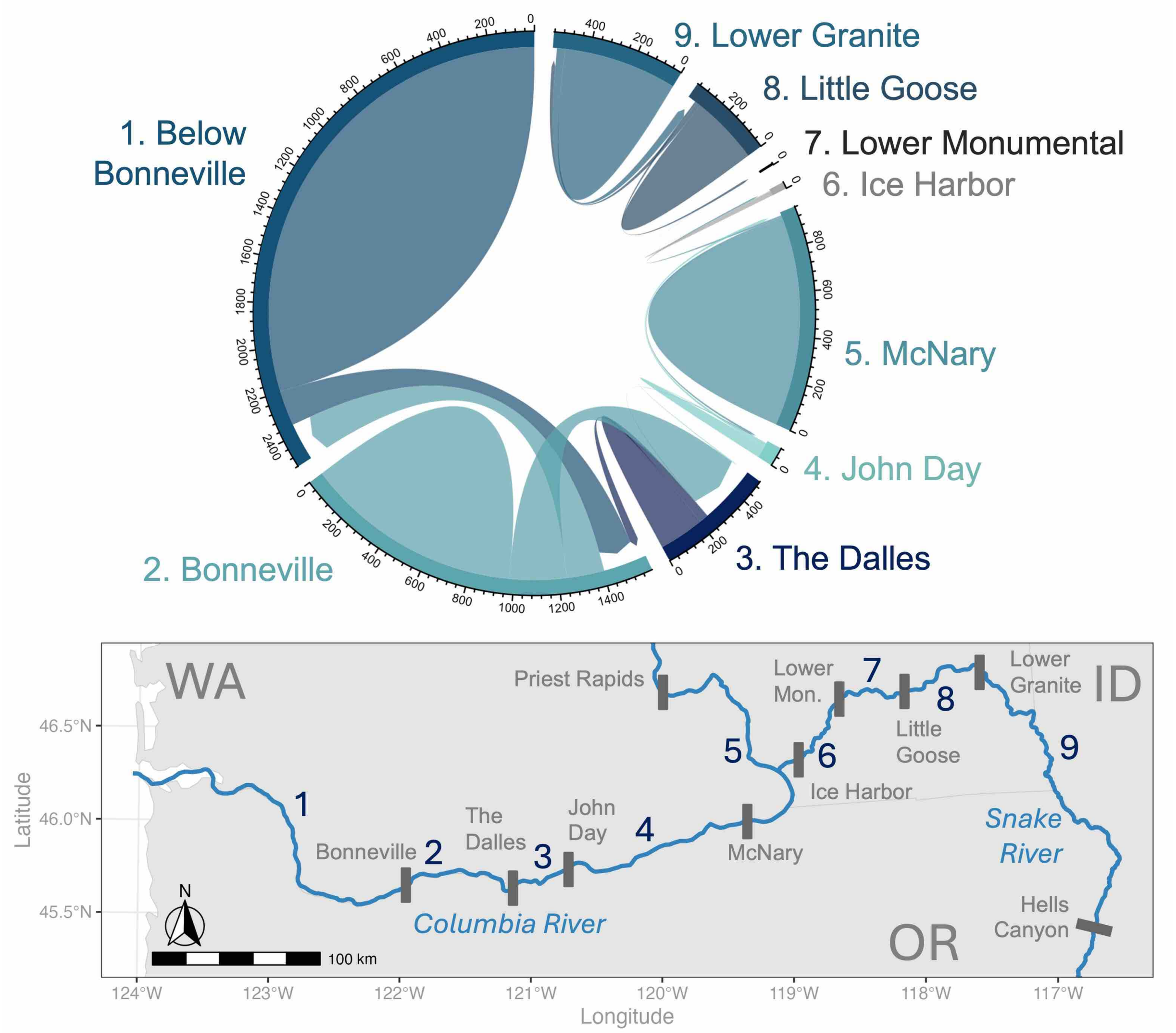


Figure 4.3: Top figure is a chord diagram displaying the movement of PIT-tagged northern pikeminnow across dams within the bounds of the Northern Pikeminnow Management Program. Each number represents a single fish and the furthest they were detected traveling. Arrows indicate movement between adjacent reaches with the thickness proportional to the number of fish. Shaded areas without arrows represent fish that were only detected in their tagged reach. Numbered labels 1-9 identify river reaches or reservoirs separated by dams (as shown in the map below).

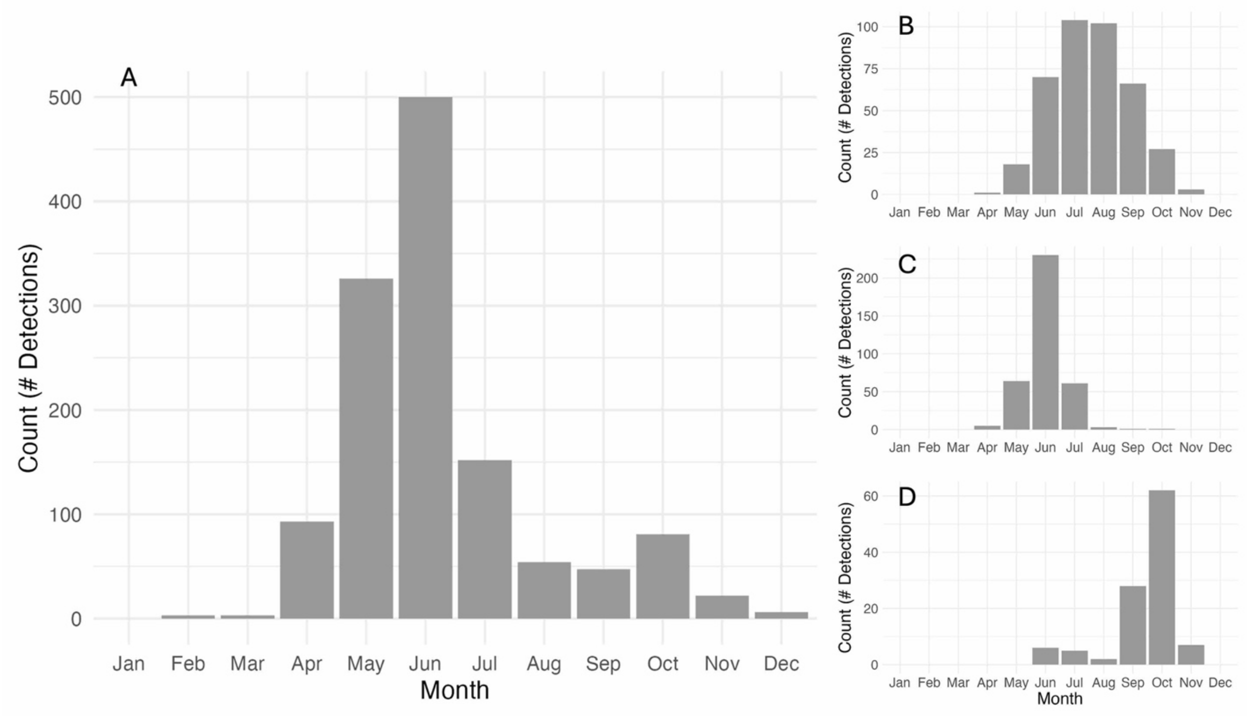
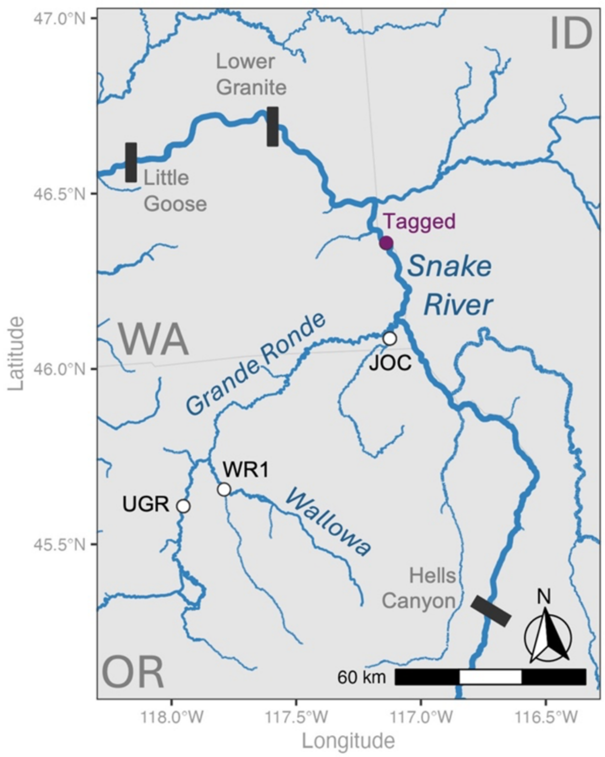


Figure 4.4: Number of detections of PIT-tagged northern pikeminnow across months of the year in all instream arrays and dam passage facilities operating year-round in tributaries (A), the Bonneville Dam adult fishway BO4 (B), the Dalles Dam adult fishway TD1 (C), and the Priest Rapids Dam adult fishway PRA (D).

Box 4.1: Furthest traveling northern pikeminnow

Twelve fish were detected traveling further than 500km after being tagged. These individuals have PIT tag records spanning the course of 3.8 - 12.4 years. One fish was detected only two times after tagging, while three fish were detected over 30 times at multiple locations. The northern pikeminnow with tag number 3DD.00773E9C20 was initially tagged in 2014 and traveled 968 km over nearly 5 years (figure and table below). This individual was tagged on the Snake River upstream of the Lower Granite Dam, with 11 subsequent detections from instream arrays on Joseph Creek and the Grande Ronde and Wallowa Rivers that operate year-round. The movements displayed a seasonal pattern wherein the fish was only detected on Joseph Creek in late April – mid June and only detected at the upper Grande Ronde site in October – November.



Site Code	Date	River
Tagged	6/14/14	Snake
JOC	6/4/15	Joseph
JOC	6/14/15	Joseph
UGR	10/18/16	Grande Ronde
JOC	5/23/17	Joseph
JOC	6/21/17	Joseph
WR1	8/1/17	Wallowa
UGR	11/28/17	Grande Ronde
JOC	4/26/18	Joseph
JOC	6/18/18	Joseph
UGR	10/12/18	Grande Ronde
JOC	5/3/19	Joseph

VITA

Jessica Diallo was born in St. Paul, Minnesota and grew up by a lake. Upon moving to Oregon in high school, she learned to row on the Willamette River. She followed her passions for rowing and science research to the University of Wisconsin-Madison where she majored in Biology in 2013. After college, she joined the Peace Corps and lived in Guinea and Mali until returning to the U.S. in 2016. While applying for graduate school, she took classes in statisics and mathematics as a non-matriculated student at the University of Washington. She began her degree at the School of Aquatic and Fishery Sciences in 2020 in the hope of becoming a government research scientist.