

Changes to the trophic structure of a desert fish community following river regulation and species turnover: implications for an endangered top predator

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Abstract

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Changes to the trophic structure of a desert fish community following river regulation and species turnover: implications for an endangered top predator

Running title: Fish community trophic changes following historic habitat alteration

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Abstract

A poor understanding of factors leading to species decline can result in inefficient or ineffective species restoration. Endangered Colorado Pikeminnow (*Ptychocheilus lucius*) was nearly extirpated from the San Juan River, NM, USA and recent efforts to reestablish the species via hatchery augmentation of juveniles has yet to reach the targeted number of adults in the system. To assess how changes to the river's food web could be limiting reestablishment of this top predator, we used stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) signatures of the fish community pre- (museum specimens) and post river regulation with coincident extirpations and invasions. Following river regulation, four of five community-wide trophic structure metrics used to quantify resource use diversity were reduced and species turnover likely had little effect per se. For species sampled in both time periods, shared trophic resources generally increased (mean niche overlap = +35.7%). However, Colorado Pikeminnow experienced a large decrease in niche breadth (-72%) and diet mixing models suggested a shift from piscivory towards insectivory in contemporary collections. Our results suggested an overall reduction in basal resource availability after river regulation. We suggest increased reliance on similar resources may be limiting fish prey for Colorado Pikeminnow, ultimately contributing to the slow and limited reestablishment in the San Juan River. This study adds to the growing body of knowledge provided by museum specimens and stable isotope analyses to identify food-web dynamics that are a departure from historical conditions which can provide novel information critical to imperiled species management in modified systems.

Keywords

Retrospective, river regulation, stable isotope, resource use

1 | INTRODUCTION

No ecosystem has escaped human alteration and a poor understanding of factors leading to species decline can result in inefficient or ineffective species restoration (Craig *et al.* , 2017; Roni *et al.* , 2018). For riverine ecosystems, major anthropogenic alterations occurred in the 20th century through dam construction, concomitant flow regulation, and establishment of nonnative fishes; all which contributed to the imperilment of many native fishes (Burkhead, 2012; Kominoski *et al.* , 2017; Lamothe and Drake, 2018). In certain cases, the primary cause of imperilment can be directly linked to nonnative fish predation (Vander Zanden *et al.* . 1999; Pelicice and Agostinho, 2009; David, 2017). In other cases when there has a poor understanding of ecosystem dynamics prior to severe habitat and species alteration, researchers may find it difficult to identify initial causes of native species declines, determine the extent to which they can be reversed, and assess trade-offs in recovery efforts (Cochran-Biederman *et al.* , 2015; Thurstan, 2022). Such knowledge gaps can also lead to extensive management efforts such as habitat manipulation (e.g., increasing structural complexity, mimicking variable flows, and reestablishment of floodplain connection) and nonnative species control that may not necessarily restore ecosystem processes needed to reestablish imperiled species if efforts are not sufficient to address proximate causes of population declines (Booth, 2016; Albertson, 2018).

Limited trophic resource availability is a potential proximate cause of some species' declines but changes to food-web dynamics can be difficult to isolate and quantify (Naiman *et al.* , 2012; Albertson *et al.* , 2018; Booth, 2016; Thoms and DeLong, 2018). The difficulty arises because changes in food-web dynamics can be mediated by synergistic indirect abiotic (habitat homogenization and fragmentation) and biotic (reduced prey diversity and abundance or competition with nonnative species) effects from river regulation and fish community compositional changes (Naiman *et al.* , 2012; Booth, 2016; Haubrock, 2018). Nevertheless, trophic resource use studies have the capacity to increase our understanding of changes in riverine food-web dynamics although there is a scarcity of unaltered systems for comparison (Turner *et al.* , 2015; McManamy *et al.* , 2018; Vander Zanden, 2003). In certain instances, species or habitat compositional gradients can be used to make comparisons but these studies are not able to detect a departure from conditions prior to

severe alterations, which might identify trophic resources that supported a more stable ecological system (Haubrock *et al.* , 2018; Rogosch and Olden, 2020; Pennock *et al.* , 2021). However, with the availability of museum specimens, use of stable isotopes, and advances in Bayesian statistical analyses, methods exist to use a hypothesis-driven framework to detect departures from a historical condition and changes to food-web dynamics that may underly the continued imperilment of native fishes (Turner *et al.* , 2015; Alp and Cucherousset, 2022).

The Colorado River Basin is a well-known example of a riverine ecosystem whose 20th century alteration resulted in the imperilment of many native fishes, including the system’s historical top predator Colorado Pikeminnow (*Ptychocheilus lucius*) (Tyus *et al.* , 1982; Minckley *et al.* 2003). In the San Juan River subbasin, Colorado Pikeminnow was nearly extirpated by the 1990s (Ryden and Ahlm, 1996; Ryden, 2003). However, 20 years of conservation management that included mimicking a more-natural hydrograph from the most upstream reservoir, intensive removal of large-bodied nonnative fishes, and a hatchery augmentation program that stocked over 5 million juvenile fish, reestablished Colorado Pikeminnow (Franssen *et al.* , 2016). Yet, the current Colorado Pikeminnow adult population is relatively small because age-specific survival rates of stocked fish are low (Clark *et al.* , 2018). A significant contribution to these low survival rates seems unlikely to be driven by nonnative fish predation as neither Colorado Pikeminnow nor more common fishes, responded positively to intensive nonnative fish removal (Franssen *et al.* , 2014); possibly because the most abundant large-bodied nonnative fish, Channel Catfish (*Ictalurus punctatus*), is not highly piscivorous (Hedden *et al.* , 2021; Pennock *et al.* , 2021; Hedden *et al.* , 2022). Additionally, attempts to mimic a more-natural hydrograph have been hampered by increased aridity in the San Juan River basin (Pennock *et al.* , 2022).

Given piscivorous Colorado Pikeminnow likely benefit from a robust fish prey base (Vanicek and Kramer, 1969), some of the slow and limited reestablishment of the species to the San Juan River could be due to trophic deficiencies caused by river regulation and species turnover (Franssen *et al.* , 2007). To assess this hypothesis, we used Bayesian methods to conduct stable isotope analyses of the river’s fish community prior to and after river regulation that was coincident with species compositional changes. To isolate the effects of species turnover, we quantified changes to community-wide trophic structure metrics (diversity of assimilated basal resources, food chain length, as well as overall resource use diversity, similarity, and distribution) with and without the inclusion of extirpated and new invasives. We then calculated changes in trophic niche overlap for fish species present before and after river regulation to explore potential changes in resource competition. To better understand any changes in both community-wide trophic structure metrics and niche overlap, we quantified changes in trophic dispersion (niche breadth). Finally, we inferred specific changes in trophic resource use of Colorado Pikeminnow between time periods using an isotopic diet mixing model.

2 | METHODS

2.1 | Study system - river regulation and fish community changes

The San Juan River is the second largest tributary in the Colorado River Basin (Thompson, 1982) and has undergone severe hydrological alteration and fragmentation (Figure 1). Construction of Glen Canyon Dam in 1957 on the Colorado River created Lake Powell inundating lower reaches of the San Juan River. The upper reaches were further fragmented by Navajo Dam, completed in 1962; and altered the river’s natural flow regime by limiting spring peak flows and elevating summer base flows (Propst and Gido, 2004). Currently, the San Juan River consists of approximately 360 km of riverine habitat. In the 1990s, river ecologists began highlighting the importance of a river’s annual peak discharge in creating fish habitat as high flows can create and maintain fish habitat through increased channel heterogeneity (Poff, 1997; Van Steeter and Pitlick, 1998). This research supported the establishment of Navajo Dam flow recommendations developed to mimic the timing, frequency, and duration of the San Juan River’s natural hydrology albeit at reduced magnitudes (Holden, 1999; Pennock *et al.* , 2022). Although Navajo Dam operators attempted to meet these flow recommendations, continued significant deviations from the natural hydrograph and the establishment of nonnative vegetation likely continued to simplify and narrow the river’s channel which precluded inundation of the floodplain (Gido *et al.* , 2013; Bassett, 2015; Franssen *et al.* , 2015).

The naturally depauperate San Juan River fish community experienced compositional changes prior to and after river regulation. Nonnative Channel Catfish (*Ictalurus punctatus*) was stocked into the Colorado River Basin for food and recreation in the late 1800s and is the second most abundant large-bodied fish in the San Juan River (Franssen *et al.*, 2016, Fuller and Neilson, 2022). Common small-bodied nonnative fishes like Fathead Minnow (*Pimephales promelas*) occupied the system prior to the closure of Navajo Dam but Red Shiner (*Cyprinella lutrensis*), which is often the most abundant small-bodied fish, likely established a population in the 1980s (Franssen *et al.*, 2015; Nico *et al.*, 2022; accession records University of New Mexico Museum of Southwestern Biology [MSB]). The native fish community consists of five large-bodied endemic Colorado River Basin species: Bluehead Sucker (*Catostomus discobolus*), Flannemouth Sucker (*Catostomus latipinnis*), endangered Razorback Sucker (*Xyrauchen texanus*), Roundtail Chub (*Gila robusta*), and endangered Colorado Pikeminnow (*Ptychocheilus lucius*). The remaining two native species are small-bodied Speckled Dace (*Rhinichthys osculus*) and Mottled Sculpin (*Cottus bairdii*). Although there are no data on fish abundances prior to construction of Navajo Dam, monitoring of an application of a lethal chemical treatment downstream of Navajo Dam in the 1960s indicated the most common species collected in this location were Flannemouth Sucker and Roundtail Chub (Olson, 1962). Due to a lack of natural recruitment, populations of Colorado Pikeminnow and Razorback Sucker only persist in the San Juan River through ongoing hatchery augmentation and Roundtail Chub is functionally extirpated (Franssen *et al.*, 2016).

2.2 | Fish tissue collection

To assess changes to the trophic structure of the San Juan River’s fish community, we obtained fish tissue for isotopic analysis from a historical period that was just prior to closure of Navajo Dam (1959 to 1961) and a contemporary period, which comprised the years 2003 – 2014. We attained historical samples (~0.5 g of white muscle) from fish accessioned to MSB (supplemental material) and used raft-mounted electrofishing and seines to collect contemporary samples (see Franssen *et al.*, 2015 for details). Contemporary tissue samples consisted of white muscle, except for Colorado Pikeminnow and Channel Catfish. For these species, we sampled approximately 5 mm² of tissue from the caudal fin. In addition to contemporary fishes, we sampled riffles and backwaters for invertebrates from the Order Ephemeroptera (~2.5 mg dry mass; Franssen *et al.*, 2019). All contemporary tissue samples were preserved in table salt in the field and rinsed before processing (Arrington and Winemiller, 2002). Apart from historical Colorado Pikeminnow, we only included species with a sample size of 10 or more. To help control for ontogenetic trophic changes within species and between periods, we restricted the minimum size of fishes analyzed to 50 mm total length (TL) and the maximum to that available from MSB (Table 1). All samples were dried at 60°C for at least 24 hours before being homogenized into powder via a mortar and pestle.

2.2 | Stable isotope analysis

We analyzed fish and invertebrate samples at the Stable Isotope Mass Spectrometry Laboratory at Kansas State University, Manhattan, KS, USA, and the Center for Stable Isotopes at the University of New Mexico, Albuquerque, NM, USA. Isotopic values were standardized between laboratories using tetramin® fish food for isotopic calibration and we reported results using the common delta notation (δ

$\delta 10^3$.

We pre-processed data prior to analyses by removing obvious outliers (i.e., $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values more than two standard deviations from taxon-specific means). Due to differences in Colorado Pikeminnow and Channel Catfish tissue types sampled between time periods (i.e., muscle tissue from historical samples and fin tissue from contemporary samples), we used mean fin-to-muscle conversions. For Colorado Pikeminnow ($\delta^{13}\text{C} = -1.29$ and $\delta^{15}\text{N} = +0.56$), we used the conversion from Franssen *et al.* (2016) and for Channel Catfish ($\delta^{13}\text{C} = -1.08$ and $\delta^{15}\text{N} = +0.58$), we used Maitland (2020). Additionally, we corrected museum specimens for the effects of formalin preservation which depletes ^{13}C by 1.0 can introduce bias into isotopic analyses because they are more depleted in ^{13}C than proteins and carbohydrates (Post *et al.*, 2007). Therefore, we corrected $\delta^{13}\text{C}$ values by the ratio of C:N in samples following Post *et al.* (2007) using the formula:

$$\delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C}_{\text{raw}} - 3.32 + 0.99 \times \text{C:N}$$

3 | DATA ANALYSIS

3.1 | Community-wide trophic structure metrics

We assessed trophic structure change between the historical and contemporary San Juan River fish community using five community-wide metrics derived to quantify and test ecologically relevant hypotheses related to food webs (Layman *et al.* , 2007; Table 2). These metrics included: $\delta^{13}\text{C}$ range (CR), $\delta^{15}\text{N}$ range (NR), centroid distance (CD), nearest neighbor distance (NND), and standard deviation of the nearest neighbor distance (SDNND). Ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are simple metrics that measure the diversity of assimilated basal resources and food chain length, respectively. Centroid distance quantifies a food web’s overall resource use diversity and is calculated as the Euclidian distance from each species’ mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to the global centroid (i.e., the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for all species). Nearest neighbor distance (NND) is a measure of the trophic similarity among species and is the mean of the shortest Euclidian distance between each species’ $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean. A food web with a smaller NND suggests trophic ecologies are similar and redundant among species while a larger NND indicates more divergent trophic niches. We also calculated the standard deviation of the NND (SDNND) because it is less influenced by sample size than NND. A comparably lower SDNND suggests differences in species’ trophic niches in a food web are more evenly distributed.

To assess differences in the five community-wide trophic structure metrics between the two periods, we used the R package *SIBER*(Jackson *et al.* , 2011) which employs a Bayesian-based Markov Chain Monte Carlo (MCMC) algorithm to produce posterior probability distributions for each metric of interest using observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. To produce these distributions, we used two chains of 4,000 iterations, discarded the first 1,000 iterations, included vague priors (a normal distribution for the mean and an inverse Wishart distribution for sigma), and tested for model convergence using the Gelman-Rubin ratio (R-hat) using the R package *coda* (Gelman and Ruben, 1992; Jackson *et al.* , 2011). All R-hat were <1.01 . For each metric, we then calculated the probability the difference between historical and contemporary period trophic metric was greater than zero by subtracting posterior probability distributions and quantified the percent of the resultant distribution that was greater than zero. To isolate effects of species turnover on changes to the trophic structure of the community, we analyzed the community with (all species sampled) and without species turnover (only the core species present in both time periods).

3.2 | Core species niche overlap and dispersion

For species present before and after river regulation (core species), we calculated species pairwise trophic overlap (i.e., niche overlap) to quantify potential changes in resource competition. We used the R statistical package *nicheROVER* which employs a Bayesian framework to estimate the directional probability that a randomly drawn individual of one species overlaps into the niche of another in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ space (Swanson *et al.* , 2015; Lysy *et al.* , 2021). We used a resampling routine of 10,000 draws to randomly sample from each species pair, maintained *nicheROVER* ’s default priors (flat Normal-Independent-Inverse-Wishart distribution), and assessed model convergence (all R-hat <1.01). From each species’ directional niche overlap posterior probability distribution, we then calculated the probability the difference between time periods was greater than zero.

To identify potential changes in the diversity of trophic resources used by individual core species (i.e., collected in both time periods), we employed the *SIBER* package which uses a Bayesian method to calculate standard ellipses areas corrected for small sample sizes (SEA_B) from observed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Jackson *et al.* , 2011). We calculated SEA_B because it can be interpreted as a species’ core isotopic niche breadth and because ellipses contain 40% of the sample, the metric can be used when samples sizes differ between populations (Jackson *et al.* , 2011; Layman *et al.* , 2012). Although SEA_B corrects for small samples, samples size < 10 are prone to underestimates (Jackson *et al.* , 2011). Therefore, we included historical Colorado Pikeminnow ($n = 6$) in our analysis with the understanding that the SEA_B estimates could be artificially low. We incorporated the same MCMC algorithm parameters used to calculate fish community-wide trophic structure metrics and assessed model convergence (all R-hat <1.01). To assess whether niche

dispersion differed for each core species, we calculated the probability the difference between historical and contemporary SEA_B posterior probability distributions were greater than zero using the same procedure described above.

3.3 | Colorado Pikeminnow diet composition

To estimate Colorado Pikeminnow contemporary and historical diet composition, we used a Bayesian stable isotope mixing model in the R package *MixSIAR* (Stock *et al.* , 2018). We used this model to estimate the posterior probability distributions of the proportion each fish and invertebrate prey contributed to Colorado Pikeminnow’s isotopic signatures. The model accounts for uncertainty resulting from multiple prey items, variation in signatures among prey and the predator, and isotopic fractionation (trophic discrimination factors) between predator and prey. However, for the mixing model to be informative, isotope signatures among prey items need to be statistically dissimilar (Stock *et al.* , 2018). Therefore, we first estimated isotopic differences in prey items using two Bayesian ANOVAs (one for $\delta^{13}C$ and one for $\delta^{15}N$) with vague priors and assessed significant differences using posterior credible intervals with the R package *brms* (Bürkner, 2017). All prey items except Flannelmouth Sucker and Speckled Dace were dissimilar by at least one isotope for both time periods but we kept all species separate with the understanding that Flannelmouth Sucker and Speckled Dace posterior probability distributions would be similar and less uniquely informative. We excluded Channel Catfish as potential prey because a laboratory feeding study suggested it is unlikely to greatly contribute to Colorado Pikeminnow’s diet (Gilbert *et al.* , 2018).

Because we lacked historical invertebrate samples, we used contemporary invertebrate samples to estimate historical invertebrate isotopic values. To do so, we assumed a mean isotopic shift in invertebrates from the contemporary to historical period but retained the variability observed in contemporary samples. Following this assumption, we estimated historical invertebrate $\delta^{13}C$ and $\delta^{15}N$ values by calculating the mean difference of $\delta^{13}C$ and $\delta^{15}N$ between periods for known invertivorous fishes (Flannelmouth Sucker, Speckled Dace, and Fathead Minnow) and then subtracted this from each contemporary invertebrate isotope value (mean value shift of $\delta^{13}C = +0.32$ and $\delta^{15}N = +3.14$).

We used one mixing model for each time period to assess changes to the resource use of Colorado Pikeminnow. To complete input data for each mixing model, we used separate trophic discrimination factors (mean and standard deviation) for potential fish prey ($[?]^{13}C = 0.82 \pm 0.10$ and $[?]^{15}N = 2.76 \pm 0.35$) and invertebrates ($[?]^{13}C = 0.83 \pm 0.29$ and $[?]^{15}N = 2.93 \pm 0.23$) as estimated by Franssen *et al.* (2017). Priors for the proportion of prey in the diet for each model included 0.05 for invertebrates with the remaining proportion distributed evenly among fish prey species. We chose these prior probabilities because the most comprehensive Colorado Pikeminnow diet study suggested the species converts entirely to piscivory by 150 mm TL (Vanicek and Kramer, 1969), although a more recent stable isotope analysis suggested invertebrates contributed to the diet of fish as large as 300 mm TL (Franssen *et al.* , 2019). We computed each mixing model with three chains of 3,000,000 iterations, discarded the first 200,000, and thinned chains by retaining every 100th draw (Stock *et al.* , 2018). We again determined model convergence (all R-hat <1.01) and report predicted posterior distributions of proportional contributions of each prey item to the diet of Colorado Pikeminnow between time periods. As with all prior analysis, we assessed changes between periods by subtracting posterior probability distributions of interests to determine the probability the difference was greater than zero.

4 | RESULTS

From each period we were able to obtain tissue for $\delta^{13}C$ and $\delta^{15}N$ analysis from six San Juan River fishes. Sample sizes for each species were smaller for the historical (n range = 6 – 13) compared to the contemporary period (n range = 23 – 385) but the size range of each species sampled was similar (Table 1). Overall, the global mean $\delta^{15}N$ of fishes increased from 9.36‰ (Figure 2). Mean $\delta^{13}C$ of fishes demonstrated less change with the historical mean of -22.67‰ the contemporary mean of -22.74‰

4.1 | Community-wide trophic structure metrics

Analysis of the fish community’s trophic structure suggested an overall reduction of trophic resource use following river regulation with a limited amount due to species turnover (Table 2). With probabilities > 0.90 , core fish species experienced reductions in both $\delta^{13}\text{C}$ (27.2% decrease in $\delta^{13}\text{C}$ range) and $\delta^{15}\text{N}$ (28.7% decrease in $\delta^{15}\text{N}$ range), assimilated less diverse trophic resources (26.2% decrease in CD), and niches became more similar (27.9% decrease in NND). When including all species, the reduction in basal resource assimilation ($\delta^{13}\text{C}$ range) decreased by 32.9%. The establishment of Red Shiner likely contributed to retaining the food chain length (probability of change in $\delta^{15}\text{N}$ range = 0.55) as it assimilated the lowest $\delta^{15}\text{N}$ values (mean $\delta^{15}\text{N} = 11.0$, $\text{SD} = 1.5$ most of the reduction (probability [?] 0.92) in degree of trophic diversity (CD) and niche similarity (NND) between time periods was due to factors other than species turnover as the average difference in the percent change between all and core species for these trophic metrics was 4.15%. The only community-wide trophic structure metric that did not change for either core (probability = 0.65) or all species (probability = 0.67) was the standard deviation in nearest neighbor distances (SDNND).

4.2 | Core species niche overlap and breadth

Most species demonstrated an increase in the overlap of their niche into another between time periods. Of the 20 species pairs, 16 had a probability [?] 0.89 of an increase in their niche overlap (Table 3). Between periods and among all species, mean niche overlap increased by 35.7%. For a given species, increases in niche overlap was highest for Channel Catfish (mean = 51.3%), followed closely by Colorado Pikeminnow (49.5%) and Speckled Dace (46.3%); whereas Fathead Minnow (25.4%) and Flannemouth Sucker (6.1%) showed limited increases in niche overlap. For Colorado Pikeminnow, the largest niche overlap increase was into the niche of Fathead Minnow (67.3%) and the least was into Channel Catfish (37.3%). For these nonnative fishes, niche overlap into Colorado Pikeminnow did not likely change between time periods (Fathead Minnow = 0.25 and Channel Catfish = 0.63 probability).

With a probability [?] 0.90, the niche breadth of four of the five core species changed between the historical and contemporary period (Table 4). Species with the largest niche breadth declines were Colorado Pikeminnow (72%) and Speckled Dace (33%). Whereas Flannemouth Sucker niche breadth likely increased by 165% and Fathead Minnow by 126%. A change in niche breadth was least likely (probability = 0.81) for Channel Catfish. Between periods and among species, the largest core niche breadth was historical Colorado Pikeminnow ($\text{SEA}_{\text{Bmean}} = 7.59$ and 95% CI = 3.29 – 17.04). Colorado Pikeminnow’s niche breadth may have been greater than all other historical species analyzed as only the size of Speckled Dace’s niche breath slightly overlapped (3.00, 1.72 – 5.31). The smallest historical niche breadth observed was Channel Catfish (1.25, 0.73 – 2.15) followed closely by Roundtail Chub (1.29, 0.71 – 2.33). In the contemporary period, the largest niche breadth occurred in Flannemouth Sucker (5.31, 3.49 – 8.08), followed by two species that had similar sized niche breadth, Red Shiner (4.32, 3.64 – 5.14) and Fathead Minnow (4.31, 3.07 – 5.97). Contemporary Channel Catfish continued to have the smallest niche breadth (1.58, 1.35 – 1.85).

4.2 | Colorado Pikeminnow diet composition

Isotopic biplots between Colorado Pikeminnow and potential prey items corrected for trophic discrimination suggested our analysis incorporated most potential prey items (Figure 3). The mixing models resulted in substantial predicted overlap in the proportion each diet item was consumed within periods (Figure 4). However, Colorado Pikeminnow demonstrated a predicted increase in invertebrate consumption (probability = 0.94) from a historical median of 2.4% (95% CI = 0.0 – 30.5%) to a contemporary median of 24.9% (18.1 – 33.2%). The diet mixing models predicted Red Shiner (median = 28.4%, 95% CI = 10.6 – 41.6%) took the place of Fathead Minnow (29.0%, 2.7 – 68.6%) as the mostly highly consumed fish prey. Consumption of Flannemouth Sucker and Speckled Dace, which was difficult to distinguish due to similar isotope values, averaged ~ 18% for each species and consumption by Colorado Pikeminnow may not have changed between periods (probabilities of 0.68 and 0.73, respectively). Prior to its extirpation and similar to other native potential prey, Roundtail Chub was predicted to have contributed ~18% (median = 17.9%, 1.5 – 53.7%) to Colorado Pikeminnow’s diet.

5 | DISCUSSION

By comparing historical and contemporary food webs in the San Juan River, we gained insight into trophic relationships among species, which supports a prior hypothesis that resources could be limiting the reestablishment of Colorado Pikeminnow in this modified system (Franssen *et al.* , 2007; Franssen *et al.* , 2019). Our results indicate the fish community reduced its overall trophic resource use, potentially increasing competition for resources, and Colorado Pikeminnow experienced a reduction in resource use likely due to a shift to feeding lower in the contemporary food web. Together, these results suggest trophic resource availability may be reducing prey fish populations, and in conjunction with the absolute loss of Roundtail Chub, could be hindering Colorado Pikeminnow’s ability to completely transition to piscivory and limit their ability to persist in the San Juan River.

Our results are consistent with other studies that demonstrated decreased resource use by fishes following river regulation (DeLong *et al.* , 2011; Turner *et al.* , 2015; Thoms and DeLong, 2018). Here we were also able to identify species turnover per se (loss of Roundtail Chub and addition of Red Shiner) as having a limited effect on this trophic contraction. The reductions in trophic resource diversity could stem from the loss of upstream inputs, limited floodplain exchange, and overall habitat simplification which can reduce primary basal and secondary consumer diversity and abundance (Vannote *et al.* , 1980; Junk *et al.* , 1989; Turner *et al.* , 2015; Ward *et al.* , 2002; Winemiller *et al.* , 2010; Zeni and Casatti, 2014). Additionally, deviations of the natural flow regime can shift macroinvertebrate communities (Bunn and Arthington, 2002), potentially altering sources of carbon incorporated into the food web (e.g., relative abundance of allochthonous shredders vs. autochthonous scrapers). The changes we observed in the San Juan River fish community’s trophic structure indicated resource sharing increased which has the potential to affect population dynamics of native fishes.

Results assessing changes to trophic niche overlap indicated competitive interactions among all species potentially intensified between time periods. Invertebrate size, abundance, and diversity can substantially decrease after dam construction and all fishes included in our analysis likely forage on invertebrates at some period of their lifetime (Bunn and Arthington, 2002; Zeni and Casatti, 2014; Caldwell *et al.* , 2018). While changes to the San Juan River invertebrate community are unknown, if invertebrate numbers are insufficient, competition for this prey could reduce overall fish abundances (Van Poorten *et al.* , 2018). Indeed, the densities of invertivorous Flannelmouth Sucker, Bluehead Sucker, Speckled Dace, and Red Shiner have declined in the San Juan River over the last two decades following ongoing deviations from the natural flow regime (Pennock *et al.* , 2022). Given the surprising and significant increase in niche overlap by Colorado Pikeminnow into all other species, this may also be indicative of a paucity of fish prey given their presumed piscivorous nature (Vanicek and Kramer, 1969; Franssen *et al.* , 2007; Franssen *et al.* , 2019). Bioenergetics modeling assessing production and current fish prey abundances could be a useful path forward in quantifying the ability of the system to support Colorado Pikeminnow, however, to be information such modeling may need to include ontological prey preferences and Colorado Pikeminnow predation rates.

Competition for resources can cause intraspecific individual specialization (Araújo *et al.* 2011; Bolnick *et al.* 2010), which may explain some trophic dispersion changes of fishes between time periods. Two trophic generalists, Flannelmouth Sucker and Fathead Minnow, able to consume algae and detritus in addition to invertebrates increased their relative niche breadth (i.e., standard ellipse area) between time periods. Although this diet flexibility could be advantageous in situations where resources are limited, if specialization is towards resources that are less energetically efficient, population abundances could decline (Floeter *et al.* , 2004). Colorado Pikeminnow and Speckled Dace decreased their diversity of resource use, which could be in response to environmental change because they are habitat (Speckled Dace; Gido *et al.* , 1997) or trophic (Colorado Pikeminnow; Vanicek and Kramer, 1969) specialists. Thus, these species may be unable to adapt when trophic resources when they become limited (Bolnick *et al.* , 2010; Araújo *et al.* , 2011; Sanchez-Hernandez *et al.* , 2021).

Results from the stable isotope mixing models suggested Colorado Pikeminnow shifted towards increased insectivory in the current food web. Although we introduced uncertainty into our finding by estimating isotopic variation of historical invertebrates, we think our results are plausible because complete piscivory

has been documented for wild-spawned Colorado Pikeminnow >150 mm TL elsewhere in the Colorado River Basin (Vanicek and Kramer, 1969) and the $\delta^{15}\text{N}$ signature of the two largest historical Colorado Pikeminnow sampled here also indicated high piscivory rates. Additionally, contemporary consumption of invertebrates was described in a previous investigation where the diet of Colorado Pikeminnow 100 – 350 mm TL in the San Juan River was estimated to be ~25% invertebrates (Franssen *et al.* , 2019). However, due to similar isotopic signatures among prey fishes, modeled results had relatively high levels of uncertainty. Further insights into prey consumption through stomach analysis may be required to identify potential prey preferences of Colorado Pikeminnow and confirm the relatively high predicted consumption of invertebrates in the current food web.

Combined, cur results suggest Colorado Pikeminnow fed on relatively few fish prey contemporarily compared to historic conditions possibly due to reduced prey fish abundances. Although historical fish prey abundances that supported Colorado Pikeminnow in the San Juan River are unknown, a shift to greater insectivory could have implications for growth and survival of stocked individuals that infrequently recruit to the adult life stage (Clark *et al.* , 2018; Franssen *et al.* , 2019). For piscivorous fishes like Colorado Pikeminnow, the ability to move through ontogeny from an invertebrate diet to more energetically efficient fish prey is necessary for rapid growth (Mittelbach and Persson, 1998) and subsequent survival (Nilsson and Brönmark, 2000; Persson *et al.* , 1996).

For piscivores like Colorado Pikeminnow, the establishment of some nonnative species could be useful in subsidizing a reduced prey base (Boltovskoy *et al.* , 2018; Maerz *et al.* , 2005). For example, our mixing models suggested Colorado Pikeminnow consumed a significant quantity of nonnative Fathead Minnow in both periods and nonnative Red Shiner in the contemporary period. Increased densities of these small-bodied nonnative fishes have been correlated with higher body condition in Colorado Pikeminnow suggesting they could be an important food source (Osmundson *in review*). Thus, managers may need to consider how reductions in these prey species could impact the availability of trophic resources for Colorado Pikeminnow.

6 | CONCLUSIONS

Given the lackluster success of reintroducing extirpated fish populations from hatchery broodstock (Cochran-Biederman *et al.* , 2015; Lamothe and Drake, 2019), managers will undoubtedly need to identify ways to improve factors that contributed to initial (and current) population declines to make long-term conservation progress. Here, we address this challenge by identifying and quantifying the relative influence of continued and new stressors on the conservation of an imperiled species. Our study suggests that further assessing whether contemporary prey abundances are limiting the establishment of Colorado Pikeminnow in the San Juan River is an important next step in identifying requisite management actions under continued river regulation and native species loss. This study further contributes to the growing understanding of trophic structure changes that may occur following river regulation (e.g., DeBoer *et al.* . 2022; DeLong *et al.* . 2011; DeLong *et al.* 2021; Thoms and DeLong, 2018; Turner *et al.* , 2015).

DATA AVAILABILITY STATEMENT

The data that support the findings are available from the corresponding author upon request.

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Tables

Table 1. The number (n), size range (total length), and bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope mean and standard deviation values of fishes and invertebrates sampled from the San Juan River, USA during a historical (H: 1959-1961) and contemporary (C: 2003-2014) period. Size data for contemporary *Pimephales promelas* were not collected but were likely <100 mm TL.

Species	Species code	H (n)	Size (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C (n)	Size (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Catostomus latipinnis</i>	CATLAT	10	52-128	-24.7 (0.7)	10.0 (0.9)	23	48-100	-22.6 (1.8)	12.1 (1.1)

Species	Species code	H (n)	Size (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C (n)	Size (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Cyprinella lutrensis</i> +	CYPLUT	-	-			134	20-65	-22.9 (1.5)	11.1 (1.1)
<i>Gila robusta</i>	GILROB	11	89-119	-22.6 (1.4)	9.5 (1.7)	-	-		
<i>Ictalurus punctatus</i> +	ICTPUN	13	62-295	-23.4 (0.5)	10.8 (0.8)	282	45-300	-21.9 (0.9)	11.1 (0.9)
<i>Pimephales promelas</i> +	PIMPRO	10	53-68	-25.6 (1.2)	8.7 (0.5)	37	-	-24.3 (1.8)	11.1 (1.1)
<i>Ptychocheilus lucius</i>	PTYLUC	6	170-590	-22.5 (1.8)	10.9 (1.7)	385	170-560	-21.7 (0.8)	13.1 (0.9)
<i>Rhinichthys osculus</i>	RHIOSC	13	51-81	-24.0 (2.2)	10.3 (1.9)	70	50-80	-24.3 (1.7)	11.1 (1.1)
Ephemeroptera	INVERT	-	-			40	-	-26.4 (2.3)	8.1 (2.1)

+ Nonnative species

Table 2. Community-wide trophic metrics derived by Layman *et al.* (2007) for the historical (1959 – 1961) and contemporary (2003-2014) San Juan River fish community: $\delta^{13}\text{C}$ range (CR), $\delta^{15}\text{N}$ range (NR), centroid distance (CD), nearest neighbor distance (NND), and standard deviation nearest neighbor distance (SDNND). Values are posterior probability distribution means, percent change of those means, and probability the difference between the posterior probability distributions was greater than zero.

Metric and description	Community composition	Historical	Contemporary	Percent change	Difference Probability
CR - diversity of basal resources	All species	2.52	1.69	-32.9%	0.97
NR - food chain length	Core species	2.32	1.69	-27.2%	0.91
	All species	2.72	2.83	4.0%	0.55
CD - degree of trophic diversity	Core species	2.72	1.94	-28.7%	0.98
	All species	1.17	0.89	-23.9%	0.99
NND - niche similarity	Core species	1.07	0.79	-26.2%	0.98
	All species	1.14	0.89	-21.9%	0.92
SDNND - distribution of similarity	Core species	1.11	0.80	-27.9%	0.93
	All species	0.35	0.38	8.6%	0.67
	Core species	0.38	0.34	-10.5%	0.65

Table 3. Historical (1959-1961) and contemporary (2003-2014) mean 95% niche overlap calculated from posterior probability distributions derived from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ obtained from fish present in the San Juan River, USA during both periods. Mean distribution difference is the mean of the difference between posterior probability distributions and probability of difference is the likelihood the difference in the distributions was greater than zero. Species codes are presented in Table 1.

Core species pairs and niche overlap direction	Historical mean 95% niche overlap	Contemporary Mean 95% niche overlap	Mean distribution difference	Probability of difference
PTYLUC into CATLAT	40.6	89.5	51.3	0.99
PTYLUC into RHIOSC	20.4	61.0	42.2	1.00
PTYLUC into ICTPUN	23.2	60.5	37.3	1.00
PTYLUC into PIMPRO	12.2	79.1	67.3	1.00
CATLAT into PTYLUC	83.1	47.0	-34.2	0.03
CATLAT into RHIOSC	42.2	50.9	0.1	0.73
CATLAT into ICTPUN	25.1	50.8	25.0	0.94
CATLAT into PIMPRO	37.5	71.4	33.4	0.96
RHIOSC into PTYLUC	48.5	71.3	23.6	0.92
RHIOSC into ICTPUN	40.8	81.4	40.4	0.99
RHIOSC into CATLAT	50.7	92.5	42.6	0.99
RHIOSC into PIMPRO	16.9	94.4	78.7	1.00
ICTPUN into PTYLUC	67.5	77.2	10.2	0.63
ICTPUN into CATLAT	49.7	98.9	48.4	0.94
ICTPUN into RHIOSC	34.8	93.9	59.4	1.00
ICTPUN into PIMPRO	11.0	97.5	87.0	1.00
PIMPRO into PTYLUC	60.0	39.9	-19.7	0.25
PIMPRO into CATLAT	45.8	73.0	27.5	0.89
PIMPRO into ICTPUN	5.4	46.0	41.1	1.00
PIMPRO into RHIOSC	6.8	58.7	52.7	1.00

Table 4. Historical (1959 – 1961) and contemporary (2003-2014) mean Bayesian standard ellipse area corrected for small samples sizes (SEA_B) calculated from San Juan River fish tissue analyzed for stable isotopes $\delta^{13}C$ and $\delta^{15}N$. For species present during both periods, SEA_B percent change and probabilities the difference in posterior distributions was greater than zero are presented.

Species	Historical	Contemporary	Percent change	Probability of difference
<i>Catostomus latipinnis</i>	2.02	5.31	165%	0.99
<i>Pimephales promelas</i> ⁺	1.88	4.31	126%	0.99
<i>Ictalurus punctatus</i> ⁺	1.25	1.58	23%	0.81
<i>Rhinichthys osculus</i>	3.00	1.98	-33%	0.90
<i>Ptychocheilus lucius</i>	7.59	2.12	-72%	0.99
<i>Gila robusta</i>	1.29			
<i>Cyprinella lutrensis</i> ⁺		4.32		

⁺ Nonnative species

Figures

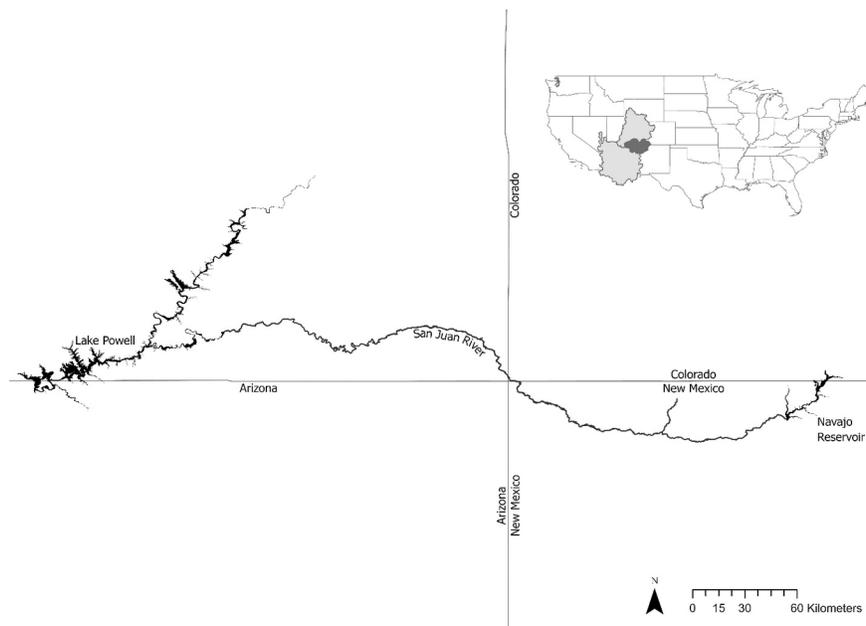


Figure 1. The San Juan River between Navajo Reservoir and Lake Powell located within the San Juan River Subbasin (inset dark grey), part of the Colorado River Basin (inset light grey).

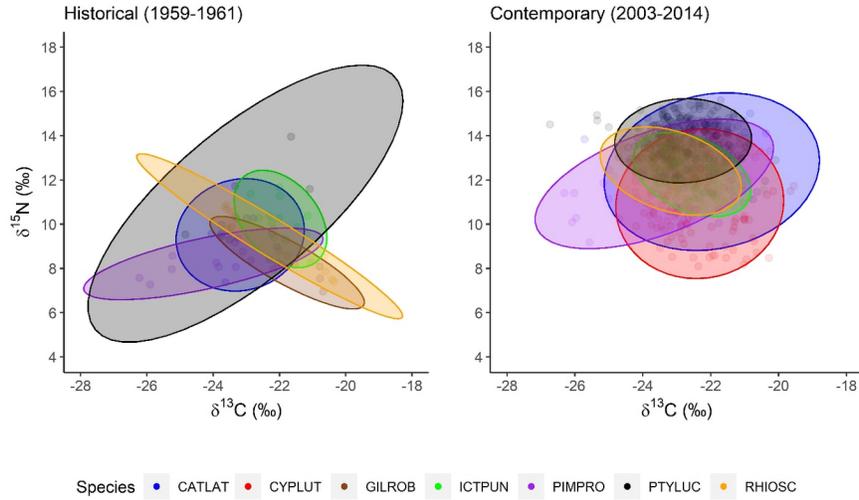


Figure 2. Stable isotope specimen values (individual dots) and standard ellipse areas calculated using 95% confidence intervals derived from fish tissue collected in the San Juan River, USA. Species codes are presented in Table 1.

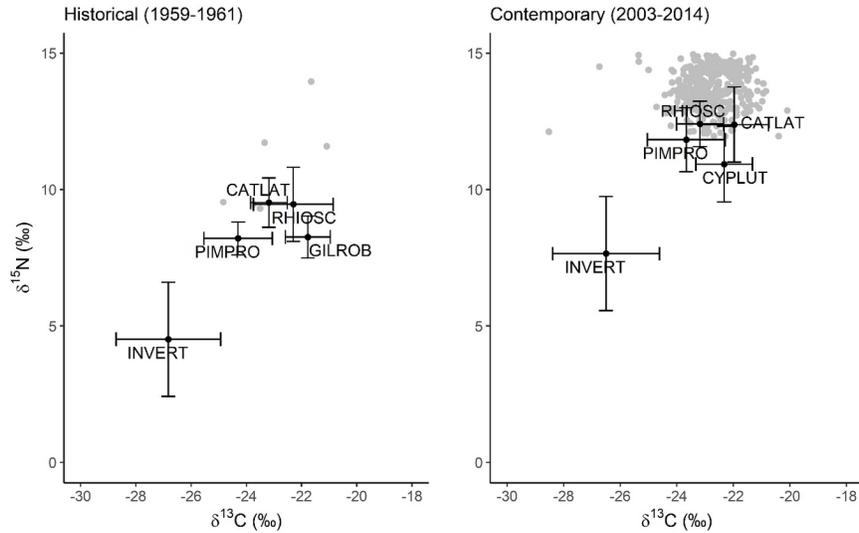


Figure 3. Bi-plots of the mean and standard error (± 1) of stable isotope values derived from Colorado Pikeminnow (grey dots) and prey tissue sampled from the San Juan River, USA. Prey values are corrected for trophic discrimination and species codes are presented in Table 1.

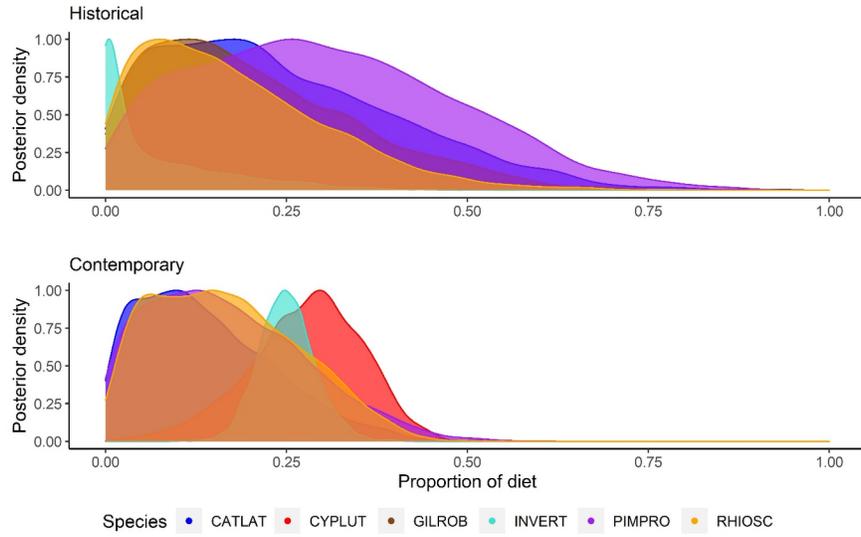


Figure 4. Scaled posterior density estimates of prey contributions to the historical (1959-1961) and contemporary (2003-2014) diet of San Juan River Colorado Pikeminnow constructed using the stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Species codes are presented in Table 1.