

ARTICLE

Threats to Rearing Juvenile Chinook Salmon from Nonnative Smallmouth Bass Inferred from Stable Isotope and Fatty Acid Biomarkers

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Abstract

Nonnative Smallmouth Bass *Micropterus dolomieu* are increasingly sympatric with juvenile spring Chinook Salmon *Oncorhynchus tshawytscha* in the rivers of western North America. Understanding the potential effects of introduced Smallmouth Bass is essential to efficiently direct salmon management efforts, especially given the potential for upstream range expansion of Smallmouth Bass in response to the climate-induced warming that many rivers may experience. However, the predatory and competitive threats of Smallmouth Bass to juvenile salmonids remain largely unexamined, particularly in salmon rearing areas. To address this knowledge gap, we collected stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and fatty acid data to assess the trophic role of Smallmouth Bass in the upstream reaches of the North Fork John Day River, a tributary of the Columbia River where the upstream invasion extent of Smallmouth Bass co-occurs with the native predator Northern Pikeminnow and river-rearing juvenile Chinook Salmon. We found that Smallmouth Bass and Northern Pikeminnow occupy divergent dietary niches, and there was little evidence of a strong predation or competition threat to juvenile Chinook Salmon from either predator. In addition, we found a disproportionate reliance on autochthonous resources across the entire community and low isotopic uniqueness, suggesting potential competition among the broader fish community given the scarcity of resources. Importantly, this study focused on the overlap between the upstream-most habitats of encroaching Smallmouth Bass and downstream-most habitats of juvenile Chinook Salmon. Therefore, the relative scarcity of rearing salmon in comparison with other available prey in this zone may limit current predation threats. The results from this study help guide resource-limited managers that are tasked with conserving and restoring native salmonid populations.

There is a long and rich history of intentionally stocking nonnative fishes to satisfy the growing recreational desires of humans (Copp et al. 2005). Fish assemblages containing nonnative species often exhibit novel food web structures, and the effects on native species can be particularly pronounced when the introduced species are top

predators (Baxter et al. 2004; Eby et al. 2006). Heightened predation pressure on native species, if sufficiently severe, can result in population decline or extirpation (Baxter et al. 2004; Eby et al. 2006; Cucherousset and Olden 2011). Beyond predation, juvenile life history stages of introduced predators also represent potential competitors to

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native species if their habitat and diet requirements overlap (Pilger et al. 2010).

Knowledge of species' trophic ecology is fundamental to understanding both predatory and competitive interactions that may arise from the introduction of nonnative species. This is increasingly accomplished through the investigation of elemental and biochemical compositions of organismal tissue, classically done by using stable isotope (SI) analyses (Sagouis et al. 2015). Stable isotope analyses estimate the relationship between the consumers and resources in a community, revealing aspects of trophic structure and dependencies on different basal resources (Layman et al. 2007; Cucherousset and Villéger 2015). Isotopic carbon reveals information about consumer energy and growth pathways, and nitrogen reveals the species' trophic levels (Post 2002). Together, carbon and nitrogen define a species' trophic position. The small number of available biomarkers (typically carbon and nitrogen, and less often, sulfur and hydrogen), however, can result in diet estimates that are largely unresolved or underdetermined, identifying prey guilds rather than individual prey species. More recently, the addition of fatty acid (FA) analyses has presented new opportunities to analyze trophic structure and diet composition (Iverson et al. 2004; Brett et al. 2016). Fatty acid analyses reveal information about consumer diets because these acids are deposited into consumer tissue with relatively little modification, and the primary producers often have distinctive FA profiles (Brett et al. 2006; O'Donovan et al. 2018). Together, SI and FA biomarkers provide insights into what the targeted consumers have eaten over ecologically relevant time scales, ranging from weeks to months, depending on the biomarker, body size, and metabolism (Post 2002; Brett et al. 2006). Simultaneous investigations that leverage the strengths of both SI and FA analyses may help resolve potential competition and predation dynamics among consumers of interest, but studies that apply both of these forms of evidence are rare.

In the Columbia River basin (CRB), native salmonids are an ecologically, culturally, and socioeconomically important species. Habitat alteration, climate change, overfishing, hatcheries, and nonnative species have contributed to dramatic declines in salmon abundance, prompting massive recovery efforts and costing the region upwards of US\$300 million annually (Naiman et al. 2012; Rieman et al. 2015; Hand et al. 2018). The current emphasis on habitat restoration, however, has yet to result in significant improvements to salmonid populations. As such, attention has pivoted towards food web approaches (Hand et al. 2018) to address the effects of nonnative species (Naiman et al. 2012). For instance, research shows that introduced predators such as Smallmouth Bass *Micropterus dolomieu*, Walleye *Sander vitreus*, and Northern Pike *Esox lucius* have increased predation pressure on

juvenile salmonids, especially during their out-migration (Vigg et al. 1991; McMahon and Bennett 1996; Zimmerman 1999; Walrath et al. 2015; Erhardt et al. 2018). In addition, studies have shown that the native CRB species, Northern Pikeminnow *Ptychocheilus oregonensis* is an efficient predator of juvenile salmonids, particularly in the presence of other nonnative predators (Rieman et al. 1991; Tabor et al. 1993; Zimmerman and Ward 1999). This has led to a massive campaign to reduce abundances of Northern Pikeminnow by using a sportfish bounty program (Carey et al. 2012). As was recently noted by the Independent Scientific Advisory Board of the Northwest Power and Conservation Council (ISAB 2019), most of the available studies examine direct predation threats to juvenile salmonids and focus on main-stem or reservoir habitats where the predation is predominantly isolated to out-migration events. By contrast, little is known regarding how nonnative and native piscivores that are sympatric with river-rearing juvenile salmonids might be compromising salmon recovery goals.

Smallmouth Bass are a popular nonnative sport fish that was first introduced into the CRB in the 1920s (Carey et al. 2011). The ensuing decades saw the range of Smallmouth Bass in the CRB broaden extensively, and their high trophic-level potential as piscivores is now cause for concern relative to salmon recovery goals (Carey et al. 2012; Rubenson and Olden 2019). Although implicated as a top predator of out-migrating salmonids in main-stem or reservoir habitats (Naughton et al. 2004; Fritts and Pearsons 2006; Erhardt et al. 2018), little is known about the predation or competition threat posed by Smallmouth Bass when they co-occur with river-rearing (age-0) salmonids in headwater habitats (Lawrence et al. 2012; ISAB 2019). Smallmouth Bass typically co-occur with Northern Pikeminnow, historically one of only a few native predators in the Columbia River (Poe et al. 1994). Before the prolific introductions of other piscivores into the CRB, Northern Pikeminnow predominantly consumed insects, crayfish, and sculpin, with only a small portion of its diet consisting of juvenile salmonids (Poe et al. 1994); all prey that may also be consumed by introduced Smallmouth Bass (Lawrence et al. 2015). The trophic interaction of nonnative Smallmouth Bass with native Northern Pikeminnow is uninvestigated in the upper parts of CRB tributaries where Smallmouth Bass co-occur with river-rearing salmonids.

Our study seeks to understand the trophic role and potential effects of nonnative Smallmouth Bass in Pacific Northwest salmon-bearing rivers to address concerns from resource-limited managers that are tasked with conserving and restoring native salmonid populations. Specifically, we sought to understand the trophic role that nonnative Smallmouth Bass play in the upstream reaches of the North Fork John Day River (hereafter, "North Fork"), a

headwater tributary of the Columbia River in northeastern Oregon. Smallmouth Bass co-occur with the native predator Northern Pikeminnow and rearing age-0 juvenile Chinook Salmon *Oncorhynchus tshawytscha* at the upstream most extent of Smallmouth Bass occurrence in the North Fork (Lawrence et al. 2012; Rubenson and Olden 2016). Our specific objectives included (1) evaluating competition between the predators Smallmouth Bass and Northern Pikeminnow where they overlap with each other and juvenile Chinook Salmon, (2) assessing the predation of these fishes on juvenile Chinook Salmon, (3) investigating whether the juvenile forms of these predators compete with each other and juvenile Chinook Salmon, and (4) examining the overall trophic structure and dependencies on different basal resources in the region of the North Fork where these species overlap seasonally. Understanding the trophic role and potential effects of nonnative Smallmouth Bass in Pacific Northwest rivers helps document how this species may be affecting salmonid recovery efforts and thus better inform and prioritize management actions that are seeking to reduce the spread and local abundance of Smallmouth Bass. Given that Smallmouth Bass occupy a large number of salmon-bearing rivers and that this number may increase with their upstream expansion as these rivers continue to warm from riparian vegetation loss and climate change, it is essential to know whether they present an additional challenge to the persistence of already threatened Pacific salmon.

METHODS

Study site and sampling effort.—The North Fork originates in the Blue Mountains of northeastern Oregon and supports one of the last remaining wild-only spring Chinook Salmon populations in the United States. Smallmouth Bass were initially introduced to the main-stem John Day River in 1971, approximately 42 km downstream of the confluence of the main stem and North Fork (Shrader and Gray 1999). Since that time, their distribution has expanded upstream, occurring as far as river kilometer (RKM) 110 in the North Fork, for a total upstream expansion of 152 km (Lawrence et al. 2012; Rubenson and Olden 2016). Age-0 juvenile Chinook Salmon emerge from their redds in the North Fork in spring (early April to mid-June; Lindsay et al. 1986). By early summer, juvenile Chinook Salmon are spread out longitudinally across the river corridor (from downstream to upstream) and are small (TL: 49–73 mm), making them vulnerable to predation (Lawrence et al. 2012). Historically age-0 juvenile spring Chinook Salmon used much of the North Fork (RKM 0–168) during the early summer (May–July; Lindsay et al. 1986). Recent surveys show that Smallmouth Bass and juvenile Chinook Salmon now share habitat between RKMs 47 and 110 (Figure 1) during early summer, with the majority of juvenile

Chinook Salmon occurring farther upstream (Lawrence et al. 2012; Rubenson and Olden 2017). Northern Pikeminnow are also present in this portion of the North Fork (RKM 47–110), but they are also distributed farther upstream (Torgersen et al. 2006). Because juvenile spring Chinook Salmon rear in-stream for one year, they are vulnerable to the competitive and predatory effects of resident species during this time.

Given that early summer is the primary opportunity for Smallmouth Bass predation on juvenile Chinook Salmon during their age-0 river-rearing phase, we focused our sampling of predators and potential prey during this time (June to early July) across the spatial area with documented overlap between these species (RKM 47–101; Lawrence et al. 2012). Specifically, 99 fish and 36 aquatic benthic invertebrate samples were collected across this spatial domain in the North Fork (Figure 1) during July 12–16, 2010, with additional aquatic benthic invertebrate ($n=7$) and terrestrial invertebrate ($n=9$) samples collected on June 26, 2013 (Table S1 available in the Supplement in the online version of this article). Sampling SI and FA at this time was intended to represent the diet patterns of our species of interest over the prior weeks and months because SI and FA temporally integrate diet over longer periods, especially compared to gut content analysis (Vander Zanden et al. 2015). The samples of predators and potential prey were concentrated primarily in two river areas, RKMs 47–52 (43%) and RKMs 69–74 (32%; Table S1). This range of RKMs (47–74) is where Smallmouth Bass are abundant. Additional samples were taken from RKMs 77–84 (12%) and RKMs 93–100 (13%), where Smallmouth Bass occur seasonally but are far less abundant. We did not sample in later summer, given that juvenile Chinook Salmon move upstream in the North Fork at that time and are therefore not vulnerable to Smallmouth Bass predation (Lawrence et al. 2012). Some Smallmouth Bass move upstream as well during late summer, but not as far upstream as juvenile Chinook Salmon. Additionally, we did not sample during the age-1 juvenile Chinook Salmon out-migration period (late February through mid-April in the North Fork; Lindsay et al. 1986), given that we were specifically interested in characterizing potential predation during the age-0 phase of life history for Chinook Salmon (a period where predation in this portion of the North Fork is more likely). In addition, Smallmouth Bass in the North Fork are less metabolically active during the out-migration period.

The SI and FA predator and prey samples included aquatic and terrestrial invertebrates, small-bodied native fishes, and our species of interest: juvenile Chinook Salmon, juvenile and adult Smallmouth Bass, and juvenile and adult Northern Pikeminnow. The potential prey items that we chose to collect were informed by the stomach content analyses of Smallmouth Bass (Lawrence et al. 2015) and Northern Pikeminnow that were conducted in

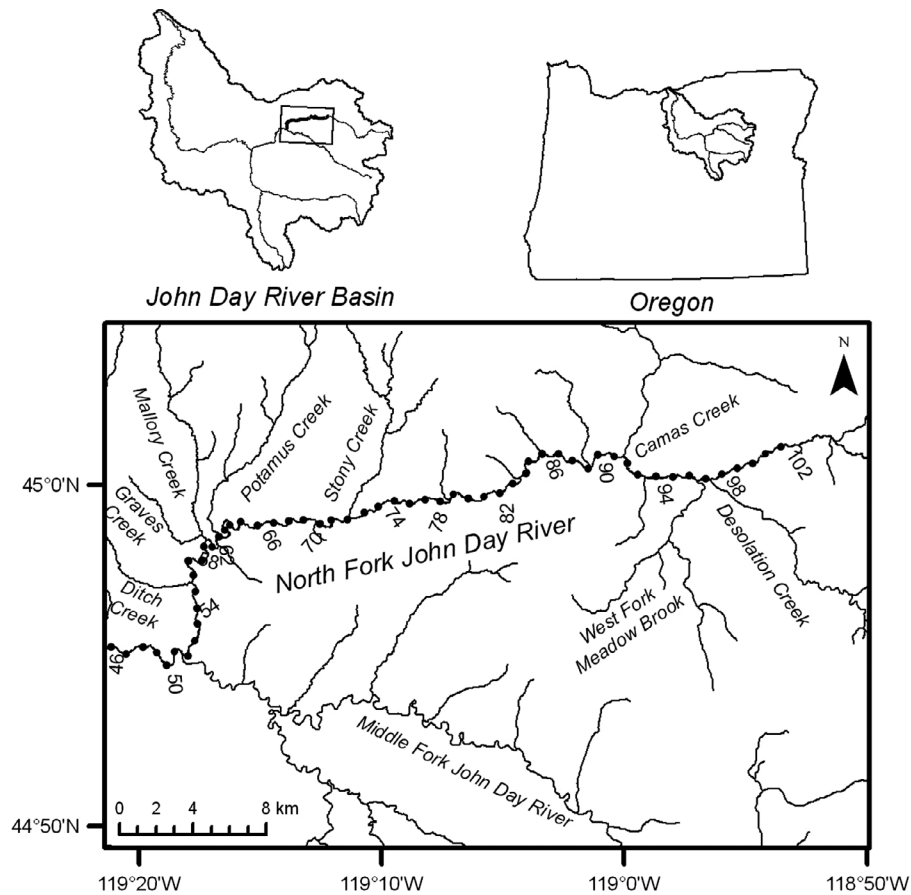


FIGURE 1. Study region depicting the North Fork John Day River (lower) and its location in Oregon, United States (upper). The box in the map of the John Day River watershed (upper left) shows the position of the North Fork map (lower). The study section is delineated by river kilometer (RKM) demarcations.

the North Fork (Oregon Department of Fish and Wildlife, unpublished data 2001–2006). Altogether, 151 samples were processed (99 fish, 43 aquatic invertebrate, and 9 terrestrial invertebrate), representing 20 species of fish, aquatic invertebrates, and terrestrial invertebrates (Table S1). Adult Smallmouth Bass (TL: 168–275 mm) and Northern Pikeminnow (TL: 207–415 mm) were collected by angling. This size range of Smallmouth Bass is representative of the most common adult size in this (cooler upstream) part of their range in the North Fork, where the vast majority (97–99%) of them were < 300 mm TL (Lawrence et al. 2012, 2015; Rubenson and Olden 2016). Smallmouth Bass and Northern Pikeminnow < 100 mm were captured by using a beach seine (see below). The adult fish were measured and weighed, and muscle tissue was harvested below the anterior dorsal fin for SI and FA analysis by using a disposable biopsy punch (Ackerson et al. 2014). The biopsied tissues were transferred to microcentrifuge tubes and placed on ice until they could be frozen. In the lab, the tissue samples were freeze-dried for 24 h in preparation for SI and FA analysis.

Potential prey items, including juvenile Smallmouth Bass (TL: 45–58 mm), juvenile Northern Pikeminnow (TL: 54–60 mm), juvenile Chinook Salmon (TL: 49–73 mm), other small-bodied fish, and crayfish were collected by using a beach seine. Macroinvertebrates were collected by hand or obtained by kick-sampling the stream bottom with a 500- μ m mesh D-net. The samples were placed on ice until they could be frozen. All of the prey samples were freeze-dried for 24 h and then ground into a powder. For the SI and FA analyses of the aquatic and terrestrial invertebrates, the individual organisms were pooled to achieve sufficient mass for chemical processing. For the statistical analysis, the aquatic invertebrates were grouped by functional feeding groups based on their life history stage when they were captured (e.g., larval versus adult), and they were assigned to collector-filterer, grazer, collector-gatherer, or predatory invertebrate groups (Table S1).

Stable isotopes.—All of the predator and potential prey samples were measured for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes by the University of California–Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer that

was interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer. The isotope composition of the samples is reported with delta values (δ) in per mille (‰) units, expressed relative to international standards Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen.

The isotopic structure of the food web was examined to determine the potential for competitive or predatory interactions between Smallmouth Bass, Northern Pikeminnow, and juvenile Chinook Salmon and to characterize the diversity of basal resources. Isotopic diversity was visualized by using isotopic biplots and quantified by calculating the metrics for isotopic richness and dispersion, following Cucherousset and Villéger (2015). These metrics are scaled between 0 and 1 to allow for mathematical independence from each other and to account for differences in sample size. Isotopic richness (IRic) is comparable to convex hull area (Layman et al. 2007) and represents the amount of isotopic space that is filled by a group of organisms. Isotopic dispersion (IDis) provides a measure of the average degree of trophic diversity in the community, trending towards 0 when all groups of species have similar stable isotope values. Competition potential was estimated by calculating the redundancy in the isotopic space, represented by an isotopic uniqueness metric (IUni; Cucherousset and Villéger 2015). Here, values close to 0 indicate that every organism shares the same isotopic space with at least one other organism, suggesting that paired species likely have similar diets. Potential species interactions were further examined by calculating the overlap in isotopic space by using the metrics isotopic similarity (ISim) and isotopic nestedness (INes), which were developed by Cucherousset and Villéger (2015). When the sample sizes of individuals of each species-group were unequal, the mean and standard deviation of the isotopic metrics were calculated by using bootstrapping. Overlap was calculated between adult Smallmouth Bass and adult Northern Pikeminnow to examine the relationship of the top two predators in the ecosystem. Similarly, overlap was evaluated between juvenile Chinook Salmon, juvenile Northern Pikeminnow, and juvenile Smallmouth Bass to estimate potential competition for basal resources.

Diets were estimated for the species of interest by using the Bayesian mixing model MixSIAR (Stock and Semmens 2016). Bayesian mixing models estimate the relative contribution (i.e., proportion) of different prey resources in the diet of a specific consumer based on the conditional probability of prey proportions given the isotopic signature of the consumer. We could determine a solution of up to three prey resources, given that our data consisted of two isotopic tracers (i.e., carbon and nitrogen). As such, all of the prey species were grouped into one of three categories: prey fish, aquatic invertebrate, or terrestrial invertebrate. The prey fish included juvenile Northern

Pikeminnow, juvenile Smallmouth Bass, juvenile Chinook Salmon, juvenile sucker species *Catostomus* spp., sculpin species *Cottus* spp., Redside Shiner *Richardsonius balteatus*, Longnose Dace *Rhinichthys cataractae*, and Speckled Dace *Rhinichthys osculus*. We used the average trophic discrimination values of $\delta^{13}\text{C} = 0.4 \pm 1.3\text{‰}$ and $\delta^{15}\text{N} = 3.4 \pm 1.0\text{‰}$ from Post (2002), which estimate the change in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from prey to predator. We included a generalist (i.e., uniform) prior for each species. Stable isotope discrimination factors may vary between species and between different diet items. In the absence of species-specific discrimination factors for our study organisms, we used the average values of Post (2002), which have been applied widely in many fisheries studies (e.g., Twardochleb and Olden 2016; Hickerson et al. 2019). Additional laboratory studies that estimate taxa-specific discrimination factors would improve the performance of SI as a food web biomarker.

The results of the mixing models were used to compare the likelihood of piscivory in adult Smallmouth Bass and Northern Pikeminnow. We also compared diets among juvenile Smallmouth Bass, Northern Pikeminnow, and Chinook Salmon to assess the potential for competition for resources between these species of interest.

Fatty acids.—The fatty acid samples were processed by following the procedures that were outlined by Brett et al. (2009). The FAs were extracted by using chloroform/methanol, followed by methylation and subsequent extraction using hexane/diethyl ether. The samples were then evaporated to dryness and resuspended in gas chromatograph-grade hexane. The analysis of the FAs was carried out in the University of Washington Lake Lab on an HP 6890 gas chromatograph with a J&W Scientific DB-23 column (30 m \times 0.25 mm, 0.15- μm film thickness), a flame ionization detector, with helium used as the carrier gas. One microliter of sample was injected. The following 85-min temperature program was used: 50°C held for 5 min, ramp at 10°C/min to 100°C, ramp at 2°C/min to 140°C, ramp at 1°C/min to 180°C, hold for 5 min, ramp at 2°C/min to 200°C, and finally, ramp at 10°C/min to 240°C. Peaks were identified based on a Supelco 37 standard from Sigma Aldrich and from past data that were gathered on the instrument and verified with gas chromatography-mass spectrometry.

Each FA was measured as the proportion of the total FA composition of each sample. Nondietary and extended-dietary FAs were removed from the data set, as determined by Iverson et al. (2004) and Budge et al. (2012). In addition, only the FAs that represented > 0.5% of the total FA composition for at least one species were retained. The remaining FAs were renormalized to 100%. The FA data were arcsine transformed before the statistical analyses were run (Budge et al. 2012). Individual outliers were assessed by using a multivariate outlier test

based on a Bray–Curtis distance matrix, examining all of the individuals that were greater than 3 SD from the mean. This resulted in two outliers being removed before the statistical analyses were conducted.

The resulting FA profiles were compared among the species to determine the amount of potential diet similarity among the species. Although FAs are generally believed to be deposited in consumer tissue with relatively little modification, some modification of these tracers is possible via consumer metabolism (Iverson et al. 2004). For some species, FA-specific calibration coefficients have been developed to account for this modification, which generally requires laboratory-based experiments (i.e., feeding specific diets to the consumers and determining the differential metabolism of the individual FAs). Because of difficulties associated with these laboratory experiments, few animals currently have an established set of calibration coefficients for FAs (Bromaghin et al. 2017), including the focal species in this work. Therefore, we treat the FA results presented here as exploratory, providing a complement to the SI data, but which could be more highly resolved if calibration coefficients become available. Consequently, we did not pursue a mixing-model equivalent to our SI work. Instead, the FA profiles of the individual fish were first visualized by using principal coordinate analysis and using a Bray–Curtis distance matrix on relative FA composition. A permutational analysis of variance and multivariate homogeneity of group variances were then conducted to test for differences in the mean and variance between target pairs of species' FA profiles (Legendre and Legendre 2012). All of the analyses were completed in R version 3.6.1 (R Foundation for Statistical Computing, Vienna).

RESULTS

We found little evidence for substantial predation from either Smallmouth Bass or native Northern Pikeminnow on juvenile Chinook Salmon, although both Smallmouth Bass and Northern Pikeminnow did appear as top trophic predators in the community. The community nitrogen-isotope values ranged from -0.48‰ to 9.77‰ , with adult Smallmouth Bass and adult Northern Pikeminnow representing the upper values (Figure 2; Table S2). The isotopic dispersion (IDis) value of 0.426, however, indicates that the isotopic values were relatively well distributed among the groups and suggests that distinct apex predators and primary consumers do not dominate the community. Instead, there is a range of species that is distributed uniformly in the nitrogen-isotope space. Juvenile Chinook Salmon, in particular, had relatively enriched nitrogen-isotope values, especially compared with other small-bodied prey fishes, adult Northern Pikeminnow, and adult Smallmouth Bass (Figure 2). The enriched nitrogen-isotope

values of juvenile Chinook Salmon contributed to the lower isotopic dispersion score, suggesting that juvenile Chinook Salmon do not constitute large portions of the adult predator species' diets. Specifically, assuming an approximate $\delta^{15}\text{N}$ fractionation rate of $3.4 \pm 1.0\text{‰}$, the relative positioning of juvenile Chinook Salmon ($\delta^{15}\text{N} = 6.7 \pm 0.3\text{‰}$) to adult Northern Pikeminnow ($\delta^{15}\text{N} = 7.6 \pm 1.0\text{‰}$) and adult Smallmouth Bass ($\delta^{15}\text{N} = 6.4 \pm 0.5\text{‰}$) is high for juvenile Chinook Salmon to be a substantial prey item for these predators. This differed from the other small-bodied fish species that had nitrogen isotopes that were closer to the expected profile of prey to adult Northern Pikeminnow and Smallmouth Bass.

There was little evidence to support substantial direct competition among our target species. We found low isotopic niche overlap between adult Northern Pikeminnow and adult Smallmouth Bass (ISim = 0.051 ± 0.005 ; INes = 0.232 ± 0.026 [Figure 3A]) and no or low overlap between the pairs of juvenile species that were examined (ISim = 0.005; INes = 0.013 for juvenile Smallmouth Bass–juvenile Northern Pikeminnow [Figure 3B], ISim = 0; INes = 0 for juvenile Northern Pikeminnow–juvenile Chinook Salmon [Figure 3C] and juvenile Smallmouth Bass–juvenile Chinook Salmon [Figure 3D]). Adult Smallmouth Bass exhibited lower nitrogen-isotope signatures relative to adult Northern Pikeminnow, suggesting that Smallmouth Bass

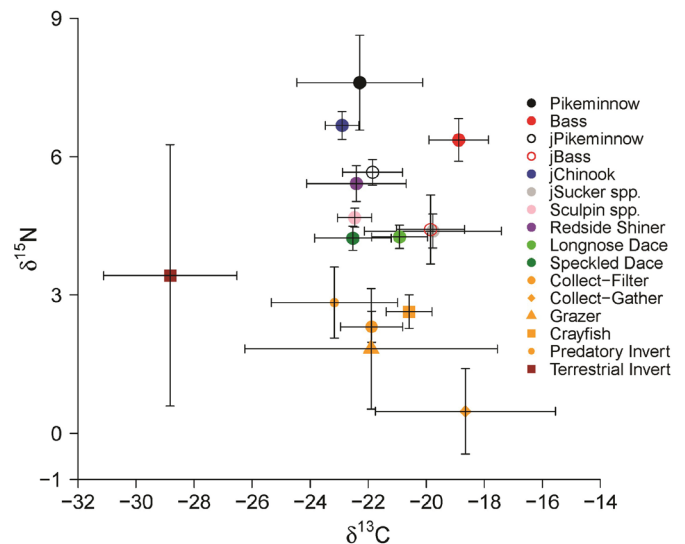


FIGURE 2. The relative position of each species-group represented in stable isotope space. The stable isotopes are represented by mean (points) and standard deviations (whiskers). The fish species include adult and juvenile Northern Pikeminnow (Pikeminnow, jPikeminnow), adult and juvenile Smallmouth Bass (Bass, jBass), juvenile Chinook Salmon (jChinook), juvenile sucker species (jSucker spp.), sculpin species (Sculpin spp.), Redside Shiner, Longnose Dace, and Speckled Dace. Aquatic insects were grouped by functional feeding groups to include collector-filterers (Collect-Filter), collector-gatherers (Collect-Gather), grazers, crayfish, predatory invertebrates, and terrestrial invertebrates. [Color figure can be viewed at afsjournals.org.]

consume more aquatic invertebrates than prey fishes relative to Northern Pikeminnow. The more enriched nitrogen-isotope signatures of juvenile Chinook Salmon differentiate it from other prey-fish species (Figure 2). The positioning of juvenile Chinook Salmon in isotopic space likely suggests some level of piscivory and/or a higher reliance on terrestrial invertebrates relative to Smallmouth Bass.

The Bayesian mixing models supported the inferences that were gleaned from the isotopic plots and metrics. Adult Northern Pikeminnow was the most piscivorous of the fishes (Figure 4A), whereas adult Smallmouth Bass appeared to rely more heavily on a mixture of aquatic invertebrates and prey fishes (Figure 4B). Juvenile Chinook Salmon (Figure 5A) appeared to be slightly differentiated from juvenile Northern Pikeminnow (Figure 5B) and juvenile Smallmouth Bass (Figure 5C) by a higher reliance on terrestrial invertebrates.

The North Fork community demonstrated high relative homogeneity of basal resources, as indicated by an

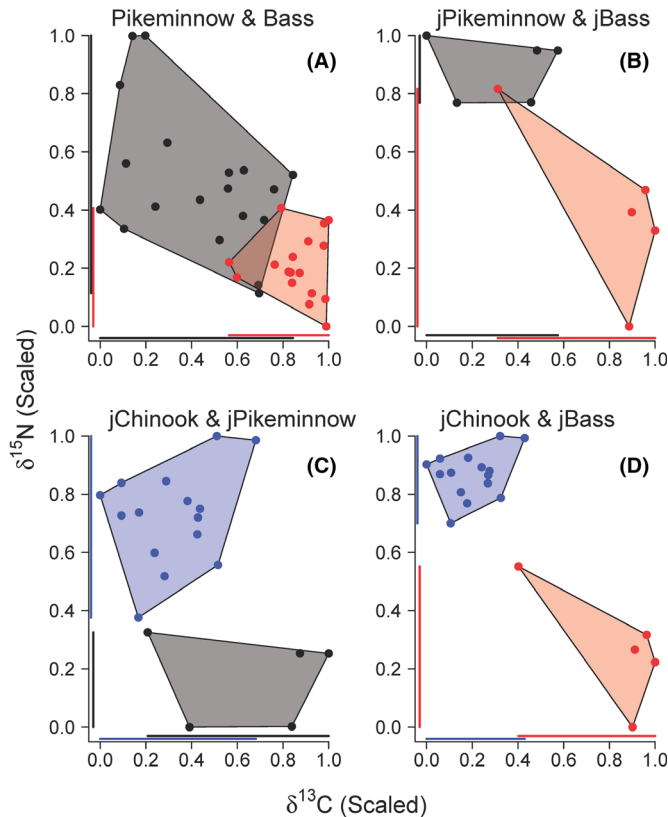


FIGURE 3. Isotopic overlap between (A) adult Northern Pikeminnow (black, Pikeminnow) and adult Smallmouth Bass (red, Bass), (B) juvenile Northern Pikeminnow (black, jPikeminnow) and juvenile Smallmouth Bass (red, jBass), (C) juvenile Chinook Salmon (blue, jChinook) and juvenile Northern Pikeminnow (black, jPikeminnow), and (D) juvenile Chinook Salmon (blue, jChinook) and juvenile Smallmouth Bass (red, jBass). The points within each polygon represent the individual samples. [Color figure can be viewed at afsjournals.org.]

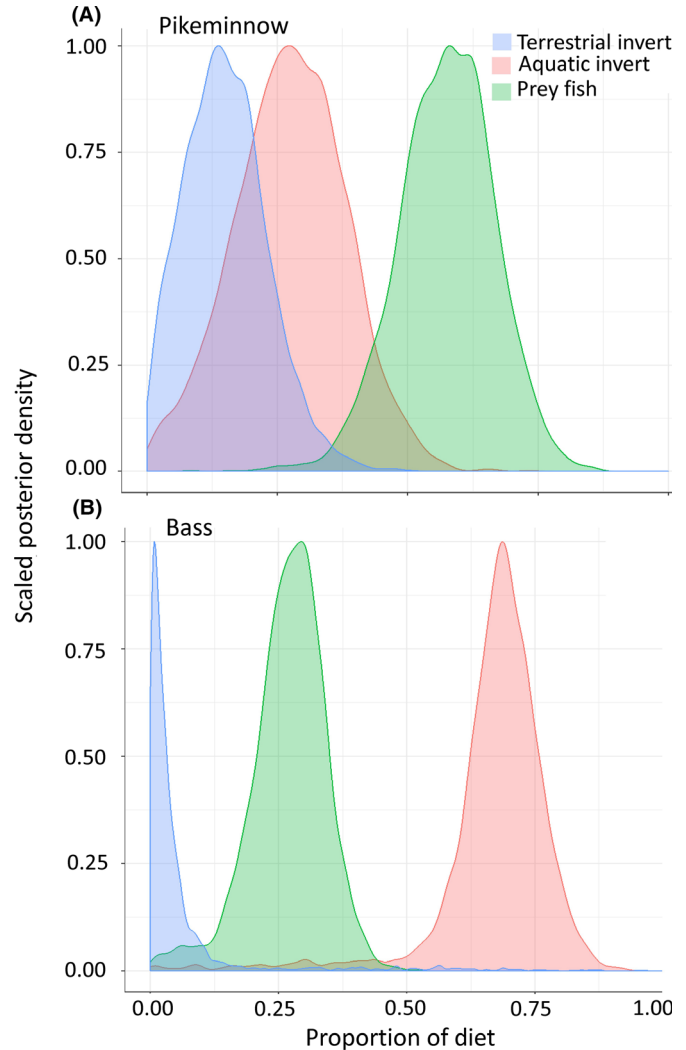


FIGURE 4. Probability distributions for the proportion of diet compositions (colors) produced from the Bayesian mixing models for (A) adult Northern Pikeminnow (Pikeminnow) and (B) adult Smallmouth Bass (Bass). The y-axis is scaled to maximize visual comparisons between disparate species. [Color figure can be viewed at afsjournals.org.]

isotopic richness (IRic) score of 0.562. This suggests a moderate degree of trophic diversity that is influenced by a few species-groups at the extremes (i.e., Northern Pikeminnow, terrestrial invertebrates, and aquatic collector-gatherers; Figure 2). The carbon isotopes showed some isotopic diversity, ranging from -14.60‰ to -31.23‰ , but the majority of the community fell within the narrower carbon-isotope range of -18‰ to -24‰ (Figure 2), indicating that the food web predominantly depends upon aquatic basal resources. In addition, an isotopic uniqueness (IUni) value of 0.268 indicates that most of the species share isotopic space with at least one other consumer. Juvenile Smallmouth Bass, in particular, appears to share isotopic space with other small-bodied fishes, with the

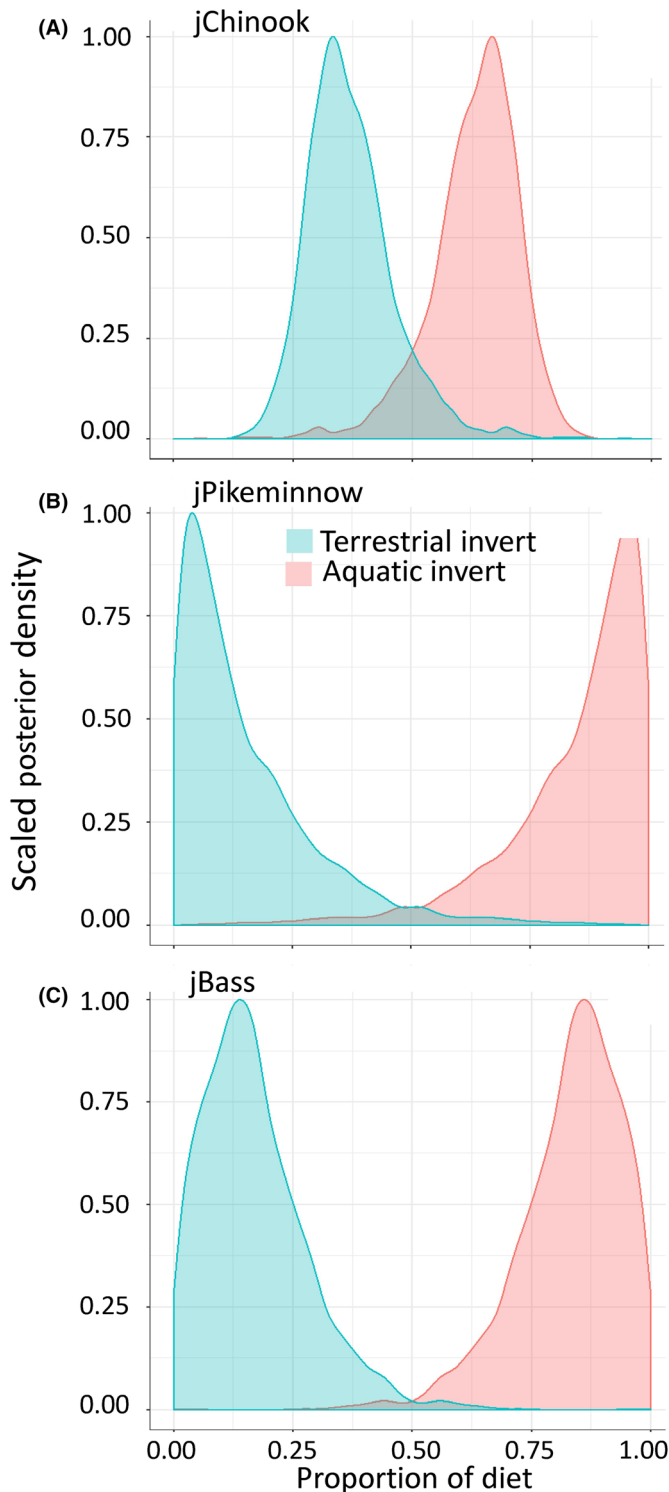


FIGURE 5. Probability distributions for the proportion of diet compositions (colors) produced from the Bayesian mixing models for (A) juvenile Chinook Salmon (jChinook), (B) juvenile Northern Pike minnow (jPike minnow), and (C) juvenile Smallmouth Bass (jBass). The y-axis is scaled to maximize visual comparisons between disparate species. [Color figure can be viewed at afs.journals.org.]

exceptions of juvenile Northern Pike minnow and juvenile Chinook Salmon (Figure 2). By contrast, adult Smallmouth Bass were more isolated in isotopic space. Overall, the combination of a homogeneous resource base and low isotopic uniqueness suggests competition among the species, with particularly high overlap between juvenile Smallmouth Bass and other small-bodied native fishes.

The FA profile of the functional feeding groups largely supported the results of the stable isotope analysis (Figures 6A, B). In total, 30 FAs were detected among the consumers of which 11 dietary FAs were retained for the analysis (Table 1). These dietary FAs were predominantly comprised of polyunsaturated FAs. The principal coordinate analysis ordination illustrates similarities in the FA profiles of individuals among the groups (Figure 6A). The FAs contributing the most to the first principal component (43% of the variation explained, $P < 0.05$) were docosahexaenoic acid (DHA; 22:6[n-3]), docosapentaenoic acid (DPA; 22:5[n-3]), and alpha-linolenic acid (ALA; 18:3[n-3]), which generally differentiated fishes, which have higher DHA and DPA (22:6[n-3] and 22:5[n-3], respectively), from invertebrates, which have higher ALA (18:3[n-3]; Figure 6A). Similar to the stable isotope analysis, adult Northern Pike minnow and adult Smallmouth Bass appeared at the top of the food web, with more enriched levels of DHA and DPA than prey fishes. Adult Smallmouth Bass demonstrated larger variance in the FA space, potentially indicating a more diversified diet (Figure 6B; Table 2). This was also true of juvenile Chinook Salmon, which had relatively large variance compared with the other species (Figure 6B; Table 2).

The FAs contributing most to the second principal component (15% of the variation explained, $P < 0.05$) were eicosapentaenoic acid (EPA; 20:5[n-3]) and linoleic acid (LIN; 18:2[n-6]). These appeared to differentiate the more benthic consumers, which have higher EPA (20:5[n-3]) from the more terrestrial consumers, which have higher LIN (18:2[n-6]; Figure 6A). Juvenile Chinook Salmon was more enriched with LIN compared with the other (more benthic) species, such as dace and sculpin that were more enriched with EPA. Juvenile Smallmouth Bass tended towards a more benthic profile, plotting relatively high on second principal component of the principal coordinate analysis ordination. Although several of the FA profiles of our target fish species demonstrated a small degree of overlap in the two-dimensional ordination plot (Figure 6B), all of the FA profiles were significantly different from one another (Table 2).

DISCUSSION

Our results suggest that nonnative Smallmouth Bass occupy a different dietary niche than the native predator

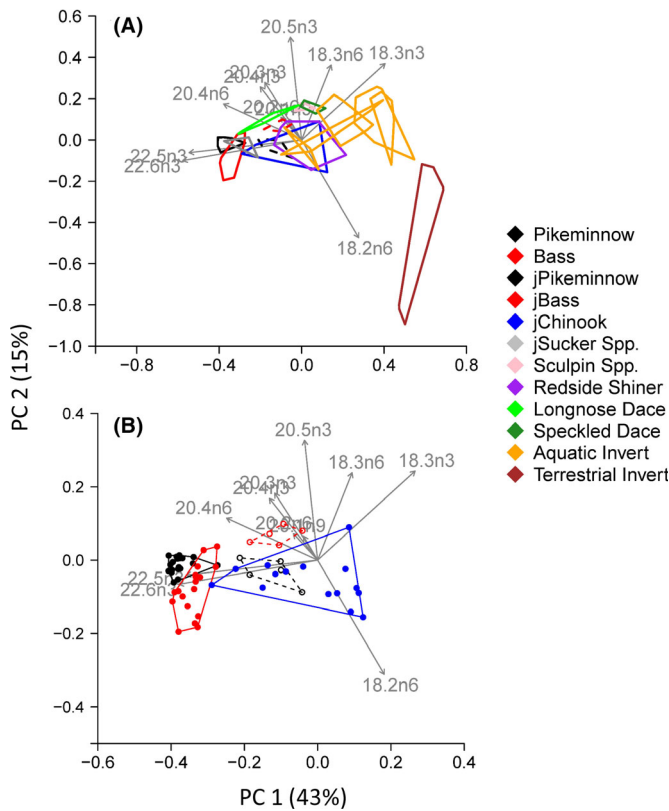


FIGURE 6. The relative position of each species or group represented in the fatty acid space according to the first two principal components of a principal coordinate analysis ordination for the (A) the entire community and (B) the target species. The convex hulls represent the entire collection of individuals, colored by species or group, whereas the points represent the individual samples (of only the target species). The species and groups are adult Northern Pikeminnow (Pikeminnow), adult Smallmouth Bass (Bass), juvenile Northern Pikeminnow (jPikeminnow), juvenile Smallmouth Bass (jBass), juvenile Chinook Salmon (jChinook), juvenile sucker species (jSucker spp.), sculpin species (Sculpin spp.), Redside Shiner, Longnose Dace, Speckled Dace, aquatic invertebrates, and terrestrial invertebrates. The dashed convex hulls represent juvenile Smallmouth Bass (red) and juvenile Northern Pikeminnow (black). [Color figure can be viewed at afsjournals.org.]

Northern Pikeminnow does in the headwaters of the North Fork, and neither predator appears to prey heavily on or compete with rearing juvenile Chinook Salmon in the river region where all three species only co-occur seasonally. This is in stark contrast to previous research that assessed predation effects in downstream habitats, where out-migrating salmonids (age 0 and 1, depending on fall or spring-type life history) comprise significant portions of Smallmouth Bass and Northern Pikeminnow diets (Tabor et al. 1993; Poe et al. 1994; Ward and Zimmerman 1999; Erhardt et al. 2018; reviewed in ISAB 2019).

As a whole, the SI and FA results were concordant, together providing a more robust assessment of the trophic effects of invasions of Smallmouth Bass into the critical

rearing habitat of salmon in headwater streams. Based on the SI and FA signature analyses, adult Smallmouth Bass appear able to successfully coexist with adult Northern Pikeminnow in the headwaters of the North Fork. This suggests that the two species increase the total predator diversity in salmon rearing habitats. Consistent with other studies in main-stem and reservoir habitats (Rieman et al. 1991; Tabor et al. 1993; Ward and Zimmerman 1999), we found that native Northern Pikeminnow is a dominant piscivore, with the most enriched SI nitrogen signature and prey fishes comprising >50% of its diet. By contrast, Smallmouth Bass appear to be less piscivorous than Northern Pikeminnow are in this headwater system, instead predominantly consuming aquatic invertebrates, with a smaller proportion of prey fishes (i.e., 10–40% of its diet). This is supported by previous diet studies that have been conducted on Smallmouth Bass in our study area, which have shown that fishes made up approximately 28–46% of stomach contents by wet weight (Lawrence et al. 2015).

The SI and FA data suggest that juvenile Chinook Salmon are not consumed by either Smallmouth Bass or Northern Pikeminnow in great quantities. However, a diet mixture that includes juvenile Chinook Salmon as prey could produce the predator $\delta^{15}\text{N}$ profiles that we observed. Predation on juvenile Chinook Salmon is possible given co-occupancy, the small size of juvenile Chinook Salmon during the period of overlap (see the size range in Methods and Lawrence et al. 2012), and the general diet preferences of Smallmouth Bass and Northern Pikeminnow that have been observed in other parts of the CRB. It is important to note, however, that juvenile Chinook Salmon are relatively scarce in the area of sympatry with Smallmouth Bass, given that this is the upstream leading edge of the Smallmouth Bass invasion and the downstream-most occurrence of juvenile Chinook Salmon (Lawrence et al. 2012; Rubenson and Olden 2017).

Beyond direct predation, the integration of Smallmouth Bass as a nonnative predator into this food web can have important indirect effects on the growth and survival of juvenile Chinook Salmon. For instance, previous research found that juvenile Chinook Salmon suffer higher stress and reduced growth in the presence of Smallmouth Bass (Kuehne et al. 2012). Smallmouth Bass have also been shown to alter the diets of other predators (Jackson 2002). Poe et al. (1994) hypothesized that Northern Pikeminnow in the lower Columbia and Snake rivers may have shifted their diet to include a higher proportion of juvenile salmonids in response to competition with nonnative predators (including Smallmouth Bass) for similar (nonsalmonid) prey. It would be informative to examine the diets of Northern Pikeminnow and growth of juvenile Chinook Salmon in habitats with and without Smallmouth Bass to assess the indirect effects that Smallmouth Bass have on rearing juvenile Chinook Salmon.

TABLE 1. Mean (SD) percentage of each dietary fatty acid for adult Northern Pikeminnow, adult Smallmouth Bass, juvenile Northern Pikeminnow (jPikeminnow), juvenile Smallmouth Bass (jBass), and juvenile Chinook Salmon (jChinook). The lipid naming follows the convention of the number to the left of the colon representing the carbon chain length, the number immediately to the right of the colon representing the number of double bonds, and number after the hyphen representing the position of the first double-bond relative to the methyl end. "Abbr." refers to the common name abbreviation for the associated fatty acid. Lipid names are defined as follows: MUFA = monounsaturated fatty acids, n-3 PUFA = omega-3 polyunsaturated acids, and n-6 PUFA = omega-6 polyunsaturated acids. The common names for the fatty acids are as follows: single asterisk "*" = eicosenoic acid, ALA = alpha-linolenic acid, ETE = eicosatrienoic acid, ETA = eicosatetraenoic acid, EPA = eicosapentaenoic acid, DPA = docosapentaenoic acid, DHA = docosahexaenoic acid, LIN = linoleic acid, GLA = gamma-linolenic acid, double asterisk "**" = eicosadienoic acid, and ARA = arachidonic acid.

Lipid name	Abbr.	Northern Pikeminnow	Smallmouth Bass	jPikeminnow	jBass	jChinook
MUFA						
20:1(n-9)	*	1.2 (0.5)	0.5 (0.6)	1.9 (1.6)	0.8 (0.6)	0.6 (1.0)
n-3 PUFA						
18:3(n-3)	ALA	4.2 (1.4)	7.3 (4.3)	11.8 (3.8)	13.9 (6.4)	22.0 (8.1)
20:3(n-3)	ETE	1.5 (0.3)	0.9 (0.9)	1.9 (0.3)	1.2 (0.6)	0.2 (0.5)
20:4(n-3)	ETA	1.5 (1.1)	1.2 (0.9)	1.4 (0.6)	1.8 (0.5)	2.1 (2.3)
20:5(n-3)	EPA	20.8 (2.5)	16.3 (3.5)	19.0 (4.5)	16.2 (4.0)	16.4 (3.0)
22:5(n-3)	DPA	7.2 (0.7)	11.1 (1.6)	5.1 (1.3)	9.6 (1.1)	4.2 (2.3)
22:6(n-3)	DHA	42.4 (5.5)	40.7 (6.7)	30.0 (8.4)	34.6 (9.3)	26.3 (11.5)
n-6 PUFA						
18:2(n-6)	LIN	5.5 (1.9)	8.6 (1.8)	17.1 (8.1)	12.5 (4.4)	23.3 (9.4)
18:3(n-6)	GLA	Trace	0.1 (0.4)	Trace	0.6 (0.4)	0.7 (2.6)
20:2(n-6)	**	1.4 (0.3)	0.3 (0.3)	2.0 (0.6)	0.6 (0.3)	Trace
20:4(n-6)	ARA	14.3 (3.0)	13.0 (2.6)	9.7 (1.5)	8.2 (2.7)	4.1 (1.3)

TABLE 2. Pairwise comparisons of fatty acid signatures between the target species: adult Northern Pikeminnow, adult Smallmouth Bass, juvenile Northern Pikeminnow (jPikeminnow), juvenile Smallmouth Bass (jBass), and juvenile Chinook Salmon (jChinook). Below the diagonal are the permutational analysis of variance results (*F*-values), with a null model of compared fatty acid signatures being the same. Above the diagonal (marked with em dashes) is a comparison of variances between species (*F*-values), with a null model of variances in compared fatty acid signatures being the same. An asterisk indicates that the species pairs are statistically different from one another ($P < 0.05$).

	Northern Pikeminnow	Smallmouth Bass	jPikeminnow	jBass	jChinook
Northern Pikeminnow	—	10.5*	0.02	1.4	22.4*
Smallmouth Bass	24.3*	—	3.9	13.4*	8.7*
jPikeminnow	50.2*	36.2*	—	0.8	5.9*
jBass	63.1*	30.7*	17.3*	—	9.2*
jChinook	77.5*	42.5*	7.2*	5.2*	—

Based on the SI analyses, we found little to no diet overlap between juvenile Smallmouth Bass, juvenile Northern Pikeminnow, and juvenile Chinook Salmon. This differentiation could be the result of at least two contrasting mechanisms. First, each species may rely on and consume different resources. Here, resource partitioning or microhabitat differences between the species may shelter juvenile Chinook Salmon from high-intensity competition with juvenile Smallmouth Bass. Second, the presence of (adult or juvenile) Smallmouth Bass could displace juvenile Chinook Salmon from their preferred diet. This could result in nonoverlapping diets and also reduce the growth potential and survival of juvenile Chinook Salmon. Historically, introduced Smallmouth Bass

are renowned for dominating resource consumption and causing significant shifts to prey availability and resource use once they are established (Vander Zanden et al. 1999; Jackson 2002). Smallmouth Bass are implicated in the substantial alteration of native assemblages of prey fish in the main-stem John Day River, where they are abundant and have established year-round presence (Hughes and Herlihy 2012). In other rivers, Smallmouth Bass have been directly implicated in the loss of native species diversity (Weyl et al. 2014). Our data demonstrate that Smallmouth Bass are well integrated into the food web of the North Fork, and they are able to capitalize on aquatic invertebrate resources that are shared among multiple consumers.

Juvenile Chinook Salmon have a high nitrogen-isotope signature relative to other small-bodied fish species in the North Fork, indicating some reliance on terrestrial inputs to the river or potential piscivory. Our Bayesian mixing model results and the position of juvenile Chinook Salmon in the FA space (i.e., in closer proximity to terrestrial resources relative to other fishes) suggest that juvenile Chinook Salmon consume terrestrial invertebrate prey more often than other potential competitors. The large variance in the FA profile for juvenile Chinook Salmon also suggests diet diversification relative to other fish species. Other studies have shown that juvenile Chinook Salmon consume both aquatic and terrestrial invertebrate prey in streams, with a preference for terrestrial invertebrates, depending on the season and conditions (Rondorf et al. 1990; Johnson 2007; Macneale et al. 2010). Juvenile Chinook Salmon may be engaging in some level of piscivory (which could elevate their $\delta^{15}\text{N}$ signature). Although not collected as potential prey items in this study, moderate levels of predation on the eggs and fry of sympatric fish species could reasonably produce elevated nitrogen-isotope levels in juvenile Chinook Salmon compared with other species.

The $\delta^{13}\text{C}$ results comparing the predator and prey samples suggest that autochthonous resources drive the food web (i.e., primarily aquatic as opposed to terrestrial) in the headwaters of the North Fork. Here, we found a relatively small difference in the carbon signatures of the fish and aquatic invertebrates but a large difference in the carbon signature of terrestrial invertebrates. The FA signature of the terrestrial invertebrates was similarly distinct relative to the food resources of the aquatic invertebrates. The carbon-depleted terrestrial invertebrate signature increases the isotopic richness of the community, but the position of the prey fishes in the carbon-isotopic space (i.e., between -18‰ and -24‰ $\delta^{13}\text{C}$) as well as the results from the Bayesian mixing models suggest that aquatic resources dominate the sampled fish diets. The FA profiles also suggest homogeneity in basal resources, with most of the fish species demonstrating similar FA compositions, whereas the terrestrial resources were distinct (and divergent) in the multivariate space. The homogeneity of basal resources and similarities in the SI and FA profiles of the individual fish species suggest a high potential for competitive interactions at a community level. The low isotopic dispersion and uniqueness scores also indicate that many of the targeted consumers share similar resources, which is supported by several species with overlapping FA profiles.

The relative positioning of the species in multivariate FA and SI space were comparable. Specifically, (1) adult Northern Pikeminnow and Smallmouth Bass were set apart from the remainder of the community, (2) the benthic-feeding prey species (i.e., Longnose Dace, Speckled Dace, sculpin species, and juvenile Smallmouth Bass) showed broad similarities, and (3) the prey species that typically feed in the

water column (i.e., Redside Shiner, juvenile Chinook Salmon, and juvenile Northern Pikeminnow) were grouped. Thus, although the FA calibration coefficients for our species are not available, the inclusion of an FA analysis provided an additional line of evidence to elucidate likely food-web interactions of a headwater stream community containing nonnative Smallmouth Bass.

Although the results of the SI and FA analyses were highly consistent, some important differences point to potential sources of uncertainty. First, the amount of overlap between some species pairs, or lack thereof, differed between the analyses. In general, the lower dimensional SI analyses (two tracers) suggested a high level of shared resources, whereas the higher dimensional FA profiles (11 tracers) revealed significant differences between species pairs, suggesting resource partitioning. The SI analyses also suggested that there is no resource overlap between juvenile Northern Pikeminnow and juvenile Chinook Salmon, whereas in FA multivariate space these species overlap. The higher dimensionality of the FA data compared with the SI data is one obvious explanation for these differences, and it is a recognized strength of examining patterns in FA composition. The inconsistencies between the SI and FA results could also be driven by unaccounted for species-specific processing and retention of lipids (i.e., FA calibration coefficients are not currently available for these species). Accounting for these differences could alter where the species are positioned relative to one another in the FA multivariate space. As such, we offer our FA analyses as exploratory, purposefully making caveated statements about the amount of shared resources or specific diets of the consumers based on the FA analysis alone. Should FA calibration coefficients for our consumers become available, these ambiguities would be better resolved, and thus help to elucidate the effects of Smallmouth Bass on juvenile Chinook Salmon and other native fishes. We urge the continued development of calibration coefficients and modeling efforts that can help derive coefficients in the absence of diet studies.

Finally, to further understand the effects of Smallmouth Bass on the native community of the North Fork, it would be informative to perform a similar investigation in habitats with the same native community, with and without Smallmouth Bass. This could help address questions, including those regarding the potential indirect effects of Smallmouth Bass on juvenile Chinook Salmon growth and whether Smallmouth Bass causes any shift in the diet of Northern Pikeminnow when these species co-occur.

IMPLICATIONS

Millions of dollars are being spent to improve the survival of juvenile salmonids in the CRB, but little research

has evaluated how salmon-bearing food webs are altered by introduced species (Naiman et al. 2012; ISAB 2019). We combined SI and FA analyses to evaluate the threat of nonnative Smallmouth Bass that are invading salmon rearing areas, with a broader goal of helping to prioritize salmon conservation efforts as their food webs change. We found that Smallmouth Bass occupy a different dietary niche than the native predator Northern Pikeminnow does in the 54-km zone of the North Fork where these species overlap with river-resident juvenile Chinook Salmon. Additionally, neither nonnative Smallmouth Bass or native Northern Pikeminnow appear to present a clear and overwhelming predatory or competitive threat to the juvenile spring Chinook Salmon population in this zone. The overlap zone represents the downstream-most habitats of juvenile Chinook Salmon and the upstream-most habitats of encroaching Smallmouth Bass (Lawrence et al. 2012; Rubenson and Olden 2017). The relative scarcity of rearing salmon in comparison to other available prey in this zone may limit current predation threats. However, stream warming that is induced by climate change is anticipated to shrink the thermally suitable habitat that is available for rearing Chinook Salmon and simultaneously allow Smallmouth Bass to move farther upstream into these rearing areas (Lawrence et al. 2014; Rubenson and Olden 2019). Thus, the threat profile of Smallmouth Bass to juvenile Chinook Salmon may change through time and should be monitored as these systems warm. Proactive actions to prevent or minimize the encroachment of Smallmouth Bass into the remaining salmonid rearing habitat may provide a currently overlooked opportunity to bolster future salmonid survival.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.