

## ARTICLE

# Age, growth, and trophic ecology of the Redeye Bass, an alien invader of California rivers

Beth Chasnoff<sup>1</sup>  | Peter B. Moyle<sup>2</sup>  | Matthew J. Young<sup>3</sup>  | Patrick K. Crain<sup>4</sup>

<sup>1</sup>Lee Vining, California, USA

<sup>2</sup>Center for Watershed Sciences and Department of Wildlife, Fisheries, and Conservation Biology, University of California, Davis, Davis, California, USA

<sup>3</sup>U.S. Geological Survey, California Water Science Center, Sacramento, California, USA

<sup>4</sup>ICF International, Sacramento, California, USA

## Correspondence

Peter B. Moyle

Email: [pmmoyle@ucdavis.edu](mailto:pmmoyle@ucdavis.edu)

[Correction added on 12 September 2024 after first online publication: The article title has been updated in this version.]

## Abstract

**Objective:** The Redeye Bass *Micropterus coosae* is a piscivore introduced into California, which has become a threat to the state's endemic freshwater fishes. It has eliminated native fishes from the middle reaches of the Cosumnes River, our study stream, which is the largest stream without a major dam on its main stem in the Sacramento–San Joaquin River drainage, central California, USA. We thoroughly documented its novel life history and ecology in California to shed light on why it has been such a successful invader despite its relatively small native range.

**Methods:** Over 4000 stable carbon and nitrogen isotope samples were utilized to refine our understanding of fish trophic position within the river food web, along with a stable isotope mixing model that accounts for uncertainty in trophic enrichment data.

**Result:** Growth was slow, with an adult size range of 9–25 cm standard length (SL), although few were larger than 15-cm SL (5–6 years old). Stable isotope analyses showed that Redeye Bass dominate the river ecosystem to the exclusion of most native fishes, occupying multiple trophic levels and microhabitats. Adults largely consumed non-native crayfish and large aquatic insects, while juveniles consumed aquatic insects, the size of prey increasing with Redeye Bass length. There was no evidence of cannibalism. Redeye Bass have effectively occupied the diverse trophic positions of at least four native fish species and have altered the trophic position of Rainbow Trout *Oncorhynchus mykiss* in sites where they co-occur with bass.

**Conclusion:** The introduction of Redeye Bass poses a continuing threat to native stream fishes in California and elsewhere.

## KEYWORDS

food webs, introduced species, invasive species, stable isotopes

## INTRODUCTION

Freshwater ecosystems are collectively the most altered ecosystems in the world (Leidy and Moyle 1997; Dudgeon et al. 2006; Reid et al. 2019), with most river systems dammed, diverted, polluted, channelized, or otherwise

permanently changed. They are also among the most invaded by alien species, especially in temperate regions (Moyle and Marchetti 2006; Light and Moyle 2015). Consequently, 50–60% of the world's freshwater fishes are estimated to face extinction in the next 50–100 years (Moyle and Leidy 2023). In California alone, 80% of the

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Transactions of the American Fisheries Society* published by Wiley Periodicals LLC on behalf of American Fisheries Society.

native freshwater fishes are either extinct or in danger of extinction in the near future (50–100 years) if present trends continue (Moyle et al. 2011, 2015; Leidy and Moyle 2021). The relative importance of habitat alteration and invasive species in causing such native fish declines is often not clear. The two factors are generally assumed to be synergistic (Light and Moyle 2015) because altered habitats favor invasive species. However, species invasions are often the primary or ultimate cause, especially if multiple alien species are involved (Light and Marchetti 2007).

The most unequivocal examples of species invasions as the main cause of native fish declines involve piscivorous fishes. In temperate habitats, black bass *Micropterus* spp. have been particularly impactful (Woodford et al. 2005; Fritts and Pearsons 2006; Takamura 2007). Black bass are native to eastern North America and have been introduced into freshwaters worldwide for sportfishing (Lever 1996). Their introduction has led to extirpations of native fish species and the homogenization of fish faunas on a landscape scale (Jackson 2002). Five species of *Micropterus* have been introduced into California: Largemouth Bass *M. nigricans*, Smallmouth Bass *M. dolomieu*, Spotted Bass *M. punctulatus*, Alabama Bass *M. henshalli*, and Redeye Bass *M. coosae*. Their spread has been associated with development of reservoirs, alteration of waterways, and introductions of other nonnative species, resulting in declines of native fishes (Moyle 2002; Moyle and Marchetti 2006). Largemouth Bass and Smallmouth Bass are particularly widespread in the state (Moyle 2002), with substantial negative impacts on native fishes in lakes and reservoirs (Moyle 2002), freshwater tidal environments (Weinersmith et al. 2019; Nobriga et al. 2021), and streams and rivers (Huntsman et al. 2022).

In these highly altered habitats, restoration to natural flow regimes is sometimes effective in stabilizing native fish communities and reducing densities of both Largemouth and Smallmouth bass (Jacinto et al. 2023). However, Redeye Bass appear to have been solely responsible for the near elimination of native fishes in the middle reaches of the Cosumnes River (Moyle et al. 2003; Chasnoff 2005), one of the few undammed rivers flowing into California's Central Valley. The success of the Redeye Bass invasion of the Cosumnes River was unexpected because the native fishes of California streams with a natural flow regime, such as the Cosumnes River, usually show a remarkable ability to resist invasions by introduced species (Baltz and Moyle 1993; Marchetti and Moyle 2001; Kiernan et al. 2012; Jacinto et al. 2023). Redeye Bass thus seem capable of becoming established in streams with various degrees of alteration throughout California, providing a major threat to native fishes (Moyle 2002; Moyle et al. 2003).

The biology of Redeye Bass is not well understood, even within its small native range, so the purpose of our study is

### Impact statement

The Redeye Bass is a predatory fish that is endemic to the Coosa River system, spanning Georgia and Alabama, in the southeastern United States, but introduced into California. It now dominates a California river ecosystem, eliminating native fishes and simplifying the food web. Its success demonstrates the unintended consequences of introducing even fish with a small native range into a region with an already stressed native fish fauna.

to document its life history and ecology in California to shed light on why it has been such a successful invader in relatively unaltered streams. We also explore whether Redeye Bass represent a continuing threat to California's declining native fishes. Specifically, we address two primary questions:

1. Do Redeye Bass in California have age and growth patterns similar to the patterns observed in the species' small native range, or has release from constraints (e.g., predators and competitors) combined with favorable environmental conditions allowed them to grow faster and larger, making them more effective predators or competitors?
2. How do the trophic ecology and habitat use of Redeye Bass change through ontogeny, including the size at which they become piscivorous? We asked this question to assess whether Redeye Bass occupy trophic positions and habitat types that are favored by multiple species of native fish, thus leading to the reduction of native fishes.

Our answers to these questions show that Redeye Bass are deeply imbedded in stream ecosystems of California and are capable of completely displacing native fishes in some situations. Our results also suggest that management actions to reduce the impact of Redeye Bass are limited.

## BACKGROUND: REDEYE BASS

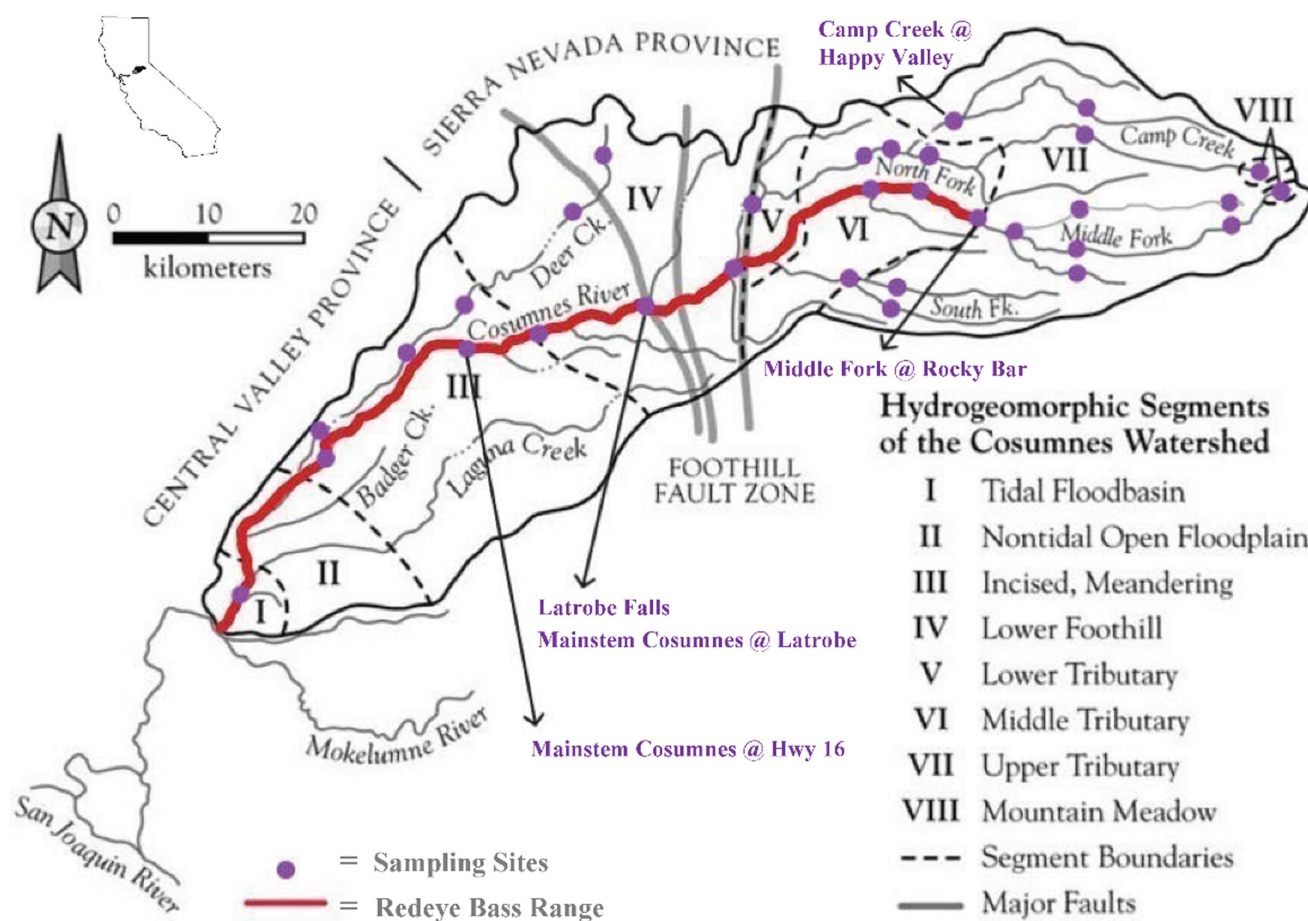
The Redeye Bass is endemic to the Coosa River, which is a major tributary to the Alabama River in Georgia and Tennessee. The name was originally applied more widely to bass in adjacent river systems as well. However, recent taxonomic studies have concluded that the Redeye Bass taxon actually encompasses five species (Page et al. 2023), including *M. coosae* (Baker et al. 2013; Leitner and Earley 2015). *Micropterus coosae* from the Coosa River watershed is the species that has been introduced

into California (Moyle 2002). Redeye Bass were introduced in 1962 and 1964 to provide angling in six small, coolwater streams that were dominated by native fishes not favored by anglers (Moyle 2002). Introductions into Dry Creek (Nevada County) and the Sisquoc River (Santa Barbara County) apparently failed. Introductions into the Stanislaus River (Tuolumne County), Feather River (Butte County), Alder Creek (Sacramento County), and Santa Margarita River (San Diego County) were successful. In 1969, they were successfully introduced into Oroville Reservoir (Butte County; Moyle 2002). Redeye Bass were unexpectedly discovered in 2000 in the Cosumnes River (El Dorado County), into which they were probably introduced shortly after the original introductions into California. Redeye Bass likely remained unnoticed for so long in the Cosumnes River because they were misidentified as Smallmouth Bass (Chasnoff 2005).

Today, Redeye Bass are found throughout the mainstem Cosumnes River and the Middle Fork Cosumnes River (Figure 1) and are the most abundant fish in the middle reaches of the river, where most native fishes have been eliminated (Moyle et al. 2003; Chasnoff 2005). Steep

boulder cascades have so far prevented Redeye Bass from moving upstream into the north fork and south fork of the Cosumnes River, which to our knowledge remain as refuges for native fishes (Moyle et al. 2003). The two native species with the greatest similarity to Redeye Bass in terms of diet and habitat are the Rainbow Trout *Oncorhynchus mykiss* and Sacramento Pikeminnow *Ptychocheilus grandis* (Moyle 2002; Chasnoff 2005), which co-occur with Redeye Bass in small numbers below the refuge areas. Other species co-occur with Redeye Bass in the lower river from Latrobe Falls to the mouth. Latrobe Falls is a long, steep boulder cascade that serves as a barrier to the anadromous fishes. It prevents “natural” upstream invasion by nonnative fishes but does not prevent Redeye Bass living above the falls from moving downstream. For a detailed description of the distribution and ecology of native and nonnative fishes in the Cosumnes River, see Moyle et al. (2003).

The life history and ecology of the Redeye Bass introduced into California are not well understood. A review of Redeye Bass biology in Alabama by Leitner and Earley (2015) did not distinguish among the recently divided taxa identified by Baker et al. (2013); therefore,



**FIGURE 1** Map of the Cosumnes River (adapted from Moyle et al. 2003), California, labeled with 32 sampling sites (purple dots) and the Redeye Bass range (red line). For additional site information, see kml file available in the [Supplementary Material](#) in the online version of this article.

species-specific life history information is sparse. In their native streams, Redeye Bass and closely related species inhabit clear, cool water with large, rocky pools, where they are opportunistic predators on fish and invertebrates, especially adult aquatic and terrestrial insects (Parsons 1954; Wright 1967; Gwinner 1973). Redeye Bass in native streams rarely reach lengths longer than 25 cm FL. They are slow growing—living 9–10 years and maturing in their second or third year (Parsons 1954; Wright 1967; Gwinner 1973).

## Study area

The Cosumnes River watershed drains 3250 km<sup>2</sup> and flows from an elevation of 2500 m in the Sierra Nevada mountains to its tidal floodplain at sea level (Moyle et al. 2003). It is the largest stream flowing into California's Central Valley without a major dam on its main stem and thus has become the focus of conservation efforts in recent years. Typical of Mediterranean climate streams, the Cosumnes River has peak flows in winter as the result of rainfall, followed by low summer flows from 5–6 months of little precipitation (Moyle et al. 2003). This study was conducted during the summer months over 3 years, when flows were typically less than about 0.28 m<sup>3</sup> s<sup>-1</sup> (10 ft<sup>3</sup> s<sup>-1</sup>) and most fish were found in large, deep pools with warm (~24–27°C), clear water.

The Coosa River, from which Redeye Bass originate, has an historic mean annual flow of 398 m<sup>3</sup> s<sup>-1</sup>; peak flows occur in March (748 m<sup>3</sup> s<sup>-1</sup>, on average), and low flows take place in September (158 m<sup>3</sup> s<sup>-1</sup> [5397 ft<sup>3</sup> s<sup>-1</sup>]). Annual variation in these flows is comparatively small (Ward et al. 2023). Average water temperatures in the main river range from 10°C in winter to 30°C or higher in summer. The Coosa River supports a high diversity of freshwater fishes (121 native species, 12 of which are endemic) as well as many native/endemic species of snails, mussels, and crayfish. The river has been highly modified by hydro-power dams, so many of these organisms are threatened with extinction. Eight species of fish in the Coosa River are listed as federally endangered (Ward et al. 2023). The Redeye Bass, while historically widespread in the system, seems to be most abundant in smaller tributary streams, which are typically cool and clear, with numerous pools and low variability in flows.

## METHODS

### Field sampling

Thirty-two sites were intensively sampled for fish, macroinvertebrates, and primary producers in the summers

of 2000, 2001, and 2002 (Figure 1; link to an interactive map of the watershed, with photographs of sampling sites [online open access]: <https://www.google.com/maps/d/edit?mid=1MDmu-m3O93LYLSJ3XmBHBagr77K9xX4U&ll=38.492788627379795%2C-120.8102246&z=10>). We chose accessible sites that represented the range of elevations within the entire watershed. Sampling sites were approximately 0.1 km in length and were selected to contain habitats (pools, riffles, and runs) spanning the range of flow conditions. Fish were captured using a Smith-Root Type 12 backpack electrofisher and dip nets, a bag seine (8-mm mesh; 10.0 × 1.3 m), and hook and line. Fish collected for this study were put on ice until they could be measured and weighed in the laboratory and prepared for scale, opercular bone, stomach content, and stable isotope analyses. Other aquatic species collected in the Cosumnes River watershed included other nonnative and native fishes, crayfish, and frogs (Table A.1). We acknowledge that the methods of capture have imperfect detection; therefore, species that were extremely low in number could have been missed during the surveys.

Invertebrates were collected from the same sites and habitats by using a Surber sampler (500-μm mesh; 0.3 × 0.3 m) or a rectangular dip net (0.5 × 0.3 m). Primary producers (i.e., terrestrial leaf litter, aquatic plants, and periphyton) were collected at each site by hand. Samples were identified immediately (under a microscope) or frozen until they could be identified and prepared for isotope analyses.

### Microhabitat

Characterization of microhabitat use by fish of all sizes followed the methods of Moyle and Baltz (1985). Redeye Bass were counted by two snorkelers, who visually estimated fish length. This method worked well for Redeye Bass because they showed little fear of observers. At the river location where a fish was observed, total depth and water velocity were measured using a flowmeter and top-setting rod. All measurements were taken in late summer (September 21–October 10, 2001), when streamflows were at their lowest (~0.28 m<sup>3</sup> s<sup>-1</sup>), at the confluence of Big Canyon Creek (just upstream of the main-stem Cosumnes River at Latrobe).

### Age and growth

Scales were removed from 177 fish and were taken below the lateral line near the pectoral fin. The scales were mounted on microscope slides and read at 23×

magnification. Ages of fish were expressed as completed years of life corresponding to the number of breaks in the otherwise continuous circuli, which were counted by two independent observers (Bonar et al. 2009). When discrepancies arose, age was averaged to the nearest half-year and fish were placed in the lower year-class for statistical analysis of age–size relationships. Annuli of opercular bones were examined from 22 fish, and length frequencies were examined for validation of age determination by the scale method. The growth rate ( $\text{mm year}^{-1}$ ) was calculated as the difference between the average standard length (SL) of all fish in successive year-classes.

## Visual diet analysis

Stomachs were removed from fresh fish and examined immediately or preserved intact in a 10% formalin solution until the stomach contents could be processed. Each individual prey item was identified to the lowest possible taxonomic level (usually order or family) and was measured using a microscope with an ocular micrometer (accurate to 0.01 mm). Dry weights of individual prey items were estimated from published length–mass regressions (Benke et al. 1999; Sabo et al. 2002).

## Isotope sample preparation

Approximately 1 g wet weight of white dorsal muscle was extracted from each adult fish specimen. Whole individuals were used for fish smaller than 40 mm SL, invertebrates, and producers. All samples were dried at 80°C for 48 h in a drying oven and were ground into a fine, homogeneous powder using mortar and pestle. Samples weighing 1.0, 1.5, and 3.0 mg (for fish, invertebrates, and producers, respectively) were packed into tin capsules (4 × 6 mm; Elemental Microanalysis Ltd.). Stable carbon and nitrogen isotope analyses were performed on the same sample using a continuous-flow Europa Hydra 20/20 isotope ratio mass spectrometer at the Stable Isotope Facility, University of California, Davis, yielding a data set of more than 4340 stable isotope results. Stable isotopes are expressed in delta notation ( $\delta$ ), defined as parts per thousand, or per mille (‰) deviation from a standard material:

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = \left[ \left( R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000, \quad (1)$$

where  $R$  is either  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$  and the standard material is the atmosphere for nitrogen and Pee Dee belemnite for carbon. The long-term standard deviation for the laboratory is 0.2‰ for  $^{13}\text{C}$  and 0.3‰ for  $^{15}\text{N}$ .

## Isotopic diet analysis

We characterized the contributions of different prey items to the Redeye Bass diet by using stable isotope mixing models (package MixSIAR version 3.1.10: Stock and Semmens 2016; program R: R Core Team 2002). This modeling technique incorporates prior information and uncertainty in source contributions, including trophic enrichment data (Moore and Semmens 2008; Phillips et al. 2014). We ran a model for two sampling locations independently, one in the upper watershed (Middle Fork Cosumnes River at Rocky Bar) and one in the lower watershed (main-stem Cosumnes River at Highway 16; Figure 1), with size-class as a categorical effect, and we used both isotope markers ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ). Each model was set to run three chains for a minimum of 100,000 Markov chain–Monte Carlo simulations, with a burn-in of 50,000 iterations for each chain.

To minimize under-determination in the mixing models, we pooled prey items into categories prior to analysis, with category assignment based on a combination of overlapping isotope values and ecological similarity. Trophic discrimination factors (TDFs; a measure of isotopic enrichment across trophic levels) were based on values for muscle tissue (McCutchan et al. 2003), with reported standard errors converted to standard deviations per MixSIAR requirements. The TDFs for this model were  $1.3 \pm 1.3\text{‰}$  for  $\delta^{13}\text{C}$  and  $2.9 \pm 1.2\text{‰}$  for  $\delta^{15}\text{N}$ .

## Relative trophic positions

Relative trophic positions of Redeye Bass were calculated to show ontogenetic shifts (changes in feeding ecology with size). To compare the trophic role of individual fish across sampling sites, trophic position was calculated per fish relative to that of the lowest  $\delta^{15}\text{N}$  values of a fish sampled at each sampling location. Examination of fish  $\delta^{15}\text{N}$  relative to a site-specific baseline was necessary because  $\delta^{15}\text{N}$  can be highly variable in space and time (Kling et al. 1992; Kline et al. 1993; Gu et al. 1994; Cabana and Rasmussen 1996; Post 2002) and may obscure variation in  $\delta^{15}\text{N}$  that reflects changes in food web structure.

We calculated relative trophic position, a continuous variable reflecting the energy-weighted mean number of feeding links between the lowest individual fish in the food web and Redeye Bass, as follows:

$$\frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}}{2.9}, \quad (2)$$

where  $\delta^{15}\text{N}_{\text{consumer}}$  is the value for the consumer,  $\delta^{15}\text{N}_{\text{baseline}}$  is the lowest  $\delta^{15}\text{N}$  value of a fish sampled at each sampling

location, and 2.9 is the average enrichment of  $\delta^{15}\text{N}$  per feeding link (McCutchan et al. 2003). Although most food chain models assume that organisms in trophic position 1 are primary producers, this model assigns primary consumers (fish) a trophic position of 0, secondary consumers are assigned a trophic position of 1, and so on, up to the top consumer.

## Stable isotope biplots

For each sampling site, biplots of stable isotope values (carbon expressed as  $\delta^{13}\text{C}$  and nitrogen expressed as  $\delta^{15}\text{N}$ ) were created with all sampled components of the food web (i.e., fish, invertebrates, and producers) to visualize food chains. Biplots of fish stable isotope values are shown for three sites where Redeye Bass were present (in the lower, middle, and upper watershed, respectively) and for one additional site where Redeye Bass were absent. These biplots illustrated four fish assemblages found in the watershed: (1) Redeye Bass co-occurring with native Sacramento Pikeminnow, (2) Redeye Bass only, (3) Redeye Bass co-occurring with native Rainbow Trout, and (4) Redeye Bass absent. In lieu of presenting plots from all sampling sites, these sites were selected because they represented the range of trophic positions of Redeye Bass throughout the watershed and allowed for comparison of the isotopic range of Redeye Bass to that of the native minnows, suckers, and trout.

At the lower limit of the Redeye Bass range (15-m elevation, main-stem Cosumnes River at Highway 16), Redeye Bass co-occur with Sacramento Pikeminnow. In the middle of their range (120-m elevation, main-stem Cosumnes River at Latrobe), Redeye Bass dominate. This is typical for most of their range in the watershed (Figure 1). Most surprisingly, all other fish species are apparently absent. California's native fishes (e.g., Sacramento Pikeminnow, California Roach *Hesperoleucus symmetricus*, Sacramento Sucker *Catostomus occidentalis*, Sacramento Speckled Dace *Rhinichthys osculus ajamawi*, and Hardhead *Mylopharodon conocephalus*) are typically abundant in these habitat conditions within California streams. At the upper limit of their range (590-m elevation, Middle Fork Cosumnes River at Rocky Bar), Redeye Bass overlap with Rainbow Trout at the downstream limit of the Rainbow Trout's range. In some tributaries within the upper watershed, native fishes dominate. One tributary to the North Fork Cosumnes River (570-m elevation, Camp Creek at Happy Valley) contains a series of major cascades yet is otherwise similar in habitat conditions to the Middle Fork Cosumnes River and its tributaries. Biplots illustrate the range of stable isotope values of all fish sampled within each site and serve to visualize energy pathways within food webs.

## RESULTS

### Age and growth

Over the 3-year study period, 257 Redeye Bass were captured and measured at 10 sites. The fish ranged from 29 to 241 mm SL, with a mean of 91 mm (Figure 2). The length-frequency distribution was highly skewed toward Redeye Bass in the 40–70-mm SL range, with less than 10% of fish measuring greater than 150 mm SL. Only five Redeye Bass greater than 200 mm SL were captured. The length–mass regression for the total population was described by the power function  $Y = 17.336X^{0.3222}$ , where  $Y$  is SL (mm) and  $X$  is mass (mg;  $N = 257$ ,  $r^2 = 0.96$ ).

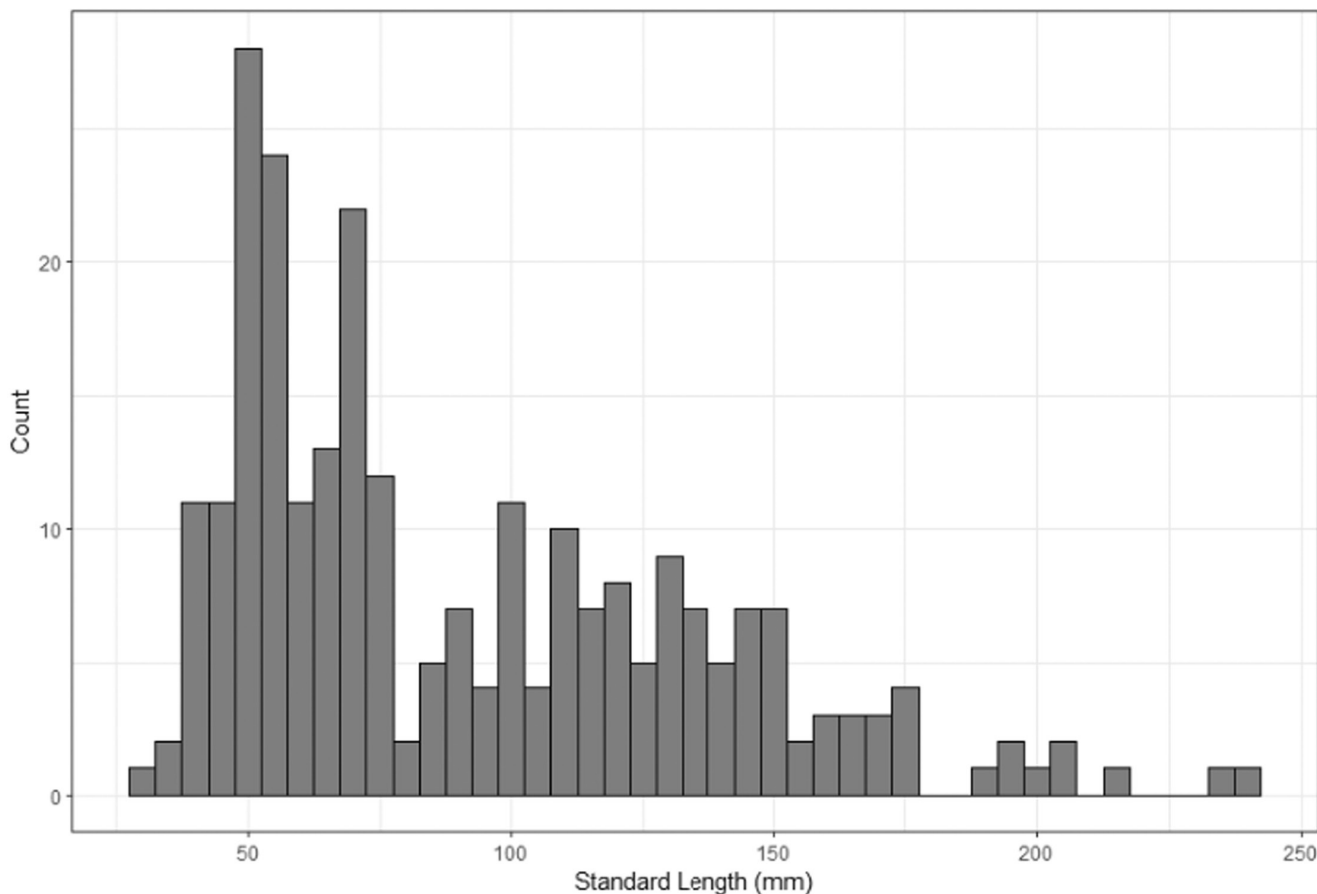
Age was determined for 177 Redeye Bass. Many (61%) age determinations differed among observers, although 98% of the discrepancies were within  $\pm 1$  year. The difficulty in finding distinct annuli presumably reflected the slow growth of the fish combined with a long growing season. Discrepancies greater than 1 year arose with three fish larger than 150 mm SL, but those individuals were most likely 6–8 years old. Age determinations based on opercular bones fell within  $\pm 1$  year of all scale counts. The relationship between size and age showed some overlap between years but suggested that length has value for estimating age (Figure 3). The length–age regression for the total population was described by the linear function  $\log_e(\text{age} + 1) = 1.064 \times \log_e(\text{SL}) - 3.612$ , where age is in years and SL is in millimeters ( $N = 177$ , adjusted  $r^2 = 0.81$ ).

### Daytime Microhabitat

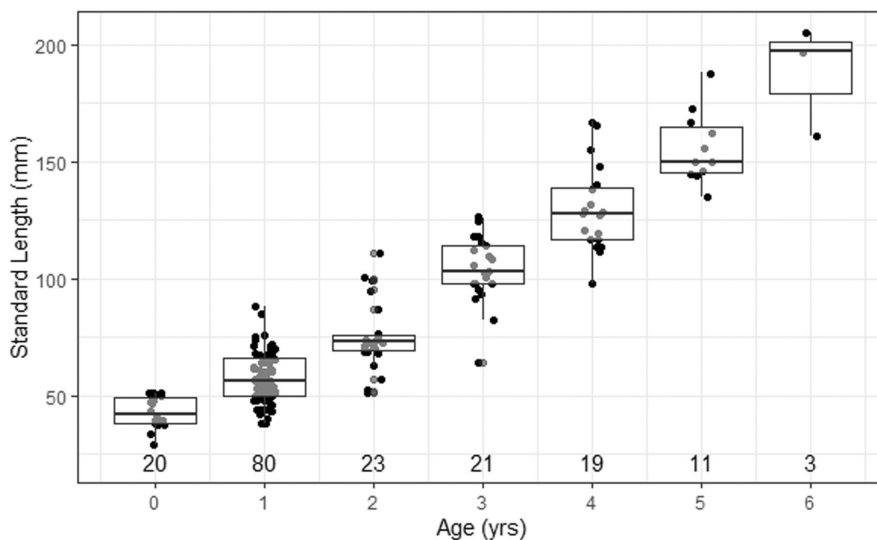
The largest Redeye Bass (>120 mm SL) dominated low-velocity, deep pools, while small bass (<75 mm) were absent from these pools and were primarily found in shallow, fast-moving riffles (Figure 4). Intermediate-sized Redeye Bass tended to be found in runs or shallow pools.

### Visual diet analysis

Prey items were identified from the stomach contents of 240 individual Redeye Bass, of which 38 were empty (Table A.2). Prey items totaling at least 1% of the diet by dry mass for large Redeye Bass included crayfish (Astacidae [Decapoda]; 89%), dobsonfly nymphs (Megaloptera; 7%), mayfly nymphs and adults (Ephemeroptera; 2%), and damselfly nymphs (Zygoptera; 2%). When analyzed across three equally divided Redeye Bass size-classes (small: <61 mm SL; medium: 61–113 mm SL; large: >113 mm SL), large fish showed several



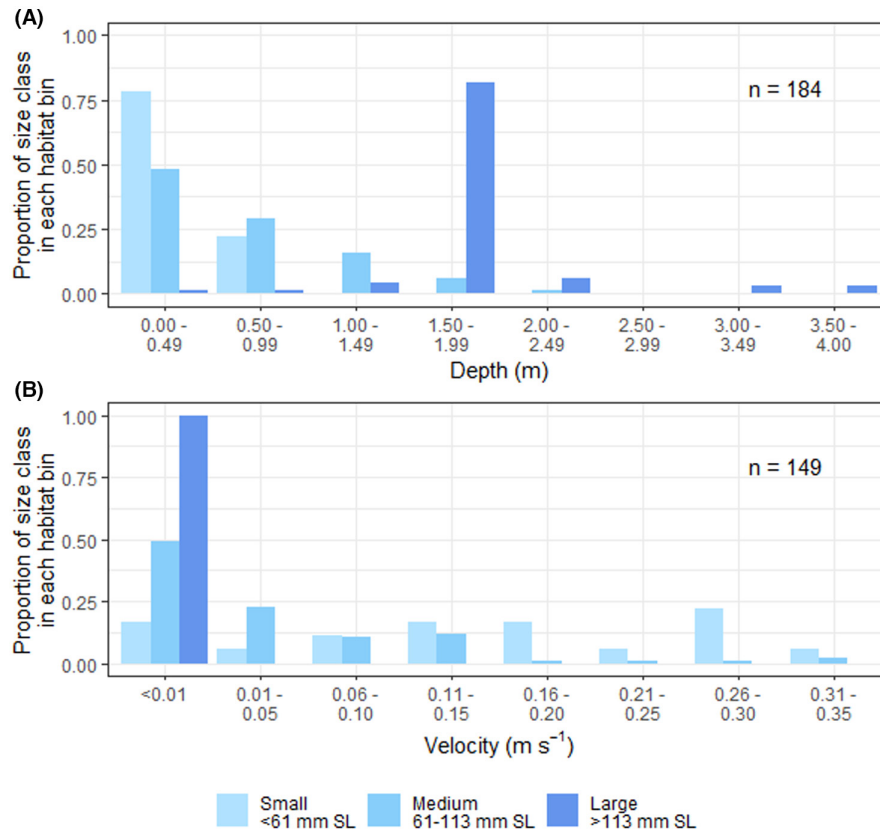
**FIGURE 2** Length-frequency histogram of Redeye Bass sampled during 2000–2002 from the Cosumnes River ( $N=257$ ; minimum length = 29 mm; maximum = 241 mm; median = 74 mm; mean  $\pm$  standard error =  $91.0 \pm 2.1$  mm).



**FIGURE 3** Average standard length (mm) by age (years) for Redeye Bass from the Cosumnes River. Sample sizes for each age-class are listed at the bottom of the figure. Box plot shows the median and interquartile ranges of all individuals (denoted by points).

differences relative to smaller size-classes. Fifty percent (38) of the stomachs from large fish were empty, while the stomachs of all smaller Redeye Bass contained food items. When the stomachs of large fish contained insects, the

insects were fewer in number (average of three prey items per stomach vs. eight prey items per stomach for other fish) but larger in size (average of 11 mm vs. 3.2 mm for other fish), with a higher frequency and proportion of crayfish



**FIGURE 4** Daytime microhabitat characteristics of individually observed Redeye Bass grouped by size-class (mm standard length [SL]): (A) depth and (B) velocity.

and dobsonfly nymphs (Figure 5). Fish were only found as prey items in the stomachs of two large Redeye Bass and included one Pacific Lamprey *Entosphenus tridentatus* ammocoete and one Prickly Sculpin *Cottus asper*.

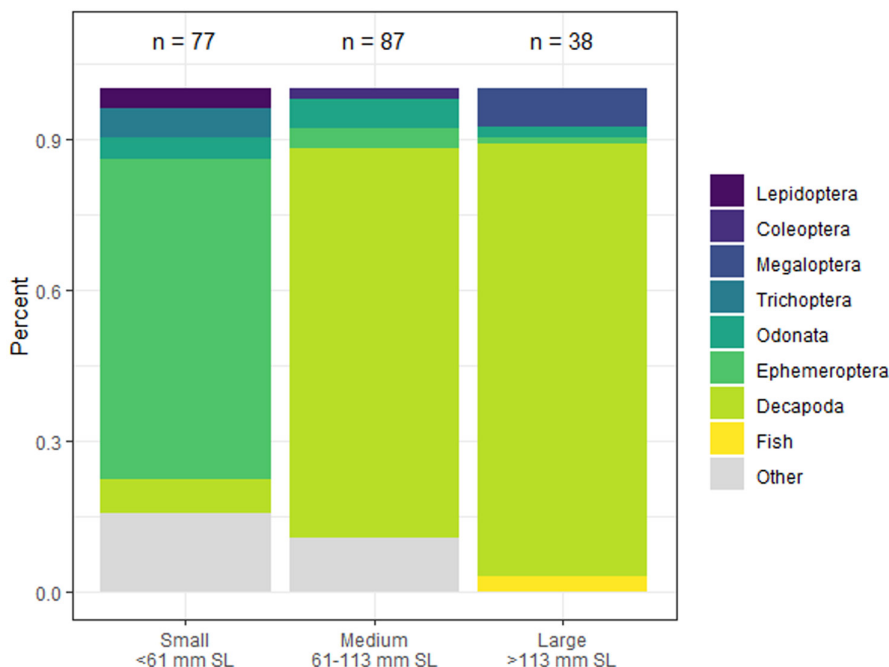
### Stable isotope diet analysis

Based on stable isotope analysis, Redeye Bass largely consumed invertebrates, particularly predatory damselflies (Odonata) and stoneflies (Plecoptera; Figure 6; Table A.3). Larger individuals were more likely to consume higher proportions of fish and crayfish (likely non-native red swamp crayfish *Procambarus clarkii*), while smaller individuals were more likely to consume true bugs (Hemiptera) and caddisflies (Trichoptera; Figure 6). Analyses of stable carbon and nitrogen in Redeye Bass and their prey items suggested that (1) large Redeye Bass were the top of the aquatic food web featuring fishes and invertebrates; (2) large Redeye Bass heavily consumed crayfish; and (3) small Redeye Bass fed primarily on herbivorous macroinvertebrates. The  $\delta^{15}\text{N}$  values of individual Redeye Bass were positively correlated with fish length, indicating that the larger bass were able to capture and ingest crayfish and large predatory macroinvertebrates (i.e., had a

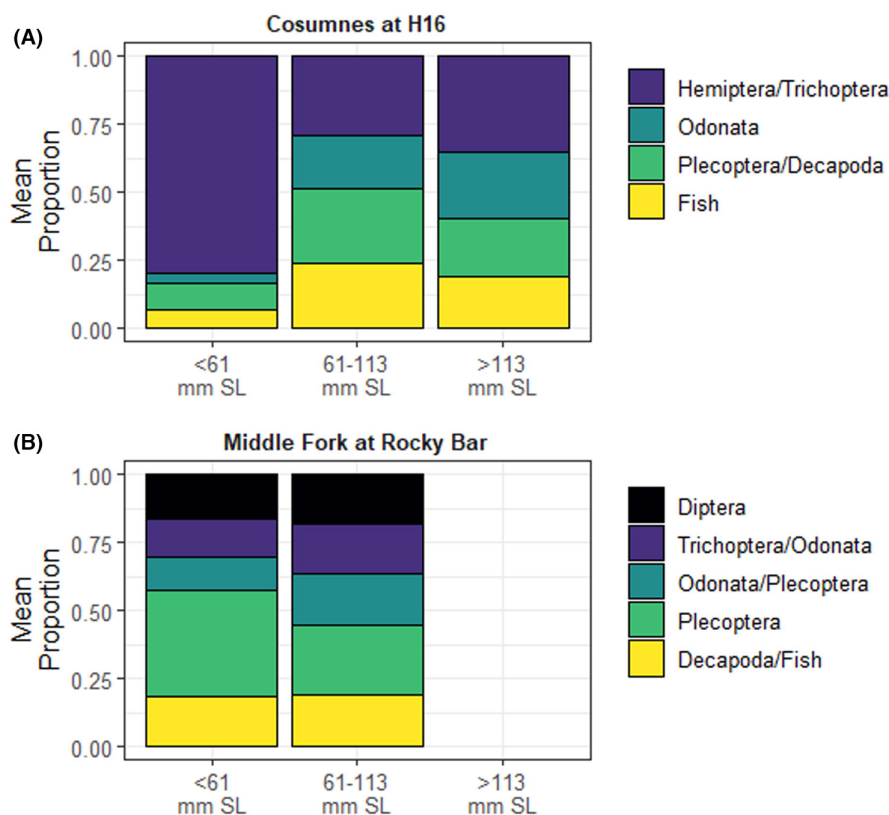
larger gape). These results were consistent with the visual analysis of stomach contents.

### Relative trophic positions

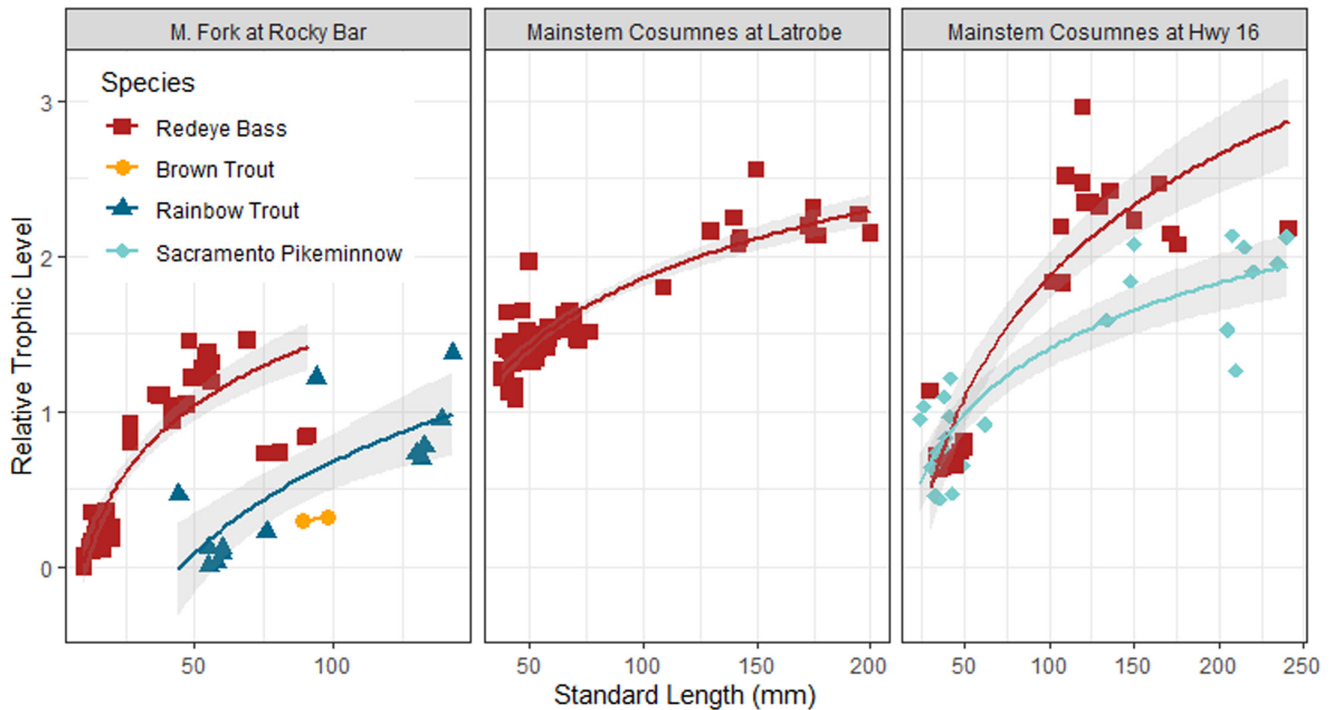
After we accounted for differences in site baseline  $\delta^{15}\text{N}$ , the relative trophic positions of Redeye Bass sampled across the watershed ranged from 0 (primary consumer) to approximately 2.5 (Figure 7). Redeye Bass generally occupied a higher relative trophic position than co-occurring fishes (Figure 7), and adult Redeye Bass typically occupied a relative trophic position that was about one level higher than the position of the smallest Redeye Bass. This indicates that larger Redeye Bass dominated the highest trophic levels in the watershed wherever they occurred. The size at which Redeye Bass are piscivorous may vary in space and time depending on prey availability, but increases in relative trophic position (Figure 7) suggested that the inclusion of fish as prey was elevated at sizes over 100 mm SL. Relative trophic positions were generally correlated with fish size, although the range of Redeye Bass relative trophic positions was consistent with an opportunistic diet, which is typical of many *Micropterus* spp. This was particularly notable when we examined the



**FIGURE 5** Prey items by percent biomass in the stomachs of Redeye Bass from three size-classes (mm standard length [SL]). The number of analyzed Redeye Bass with prey in their stomachs (*n*) is provided above each bar. A more detailed description of Redeye Bass prey items is provided in Table A.2.



**FIGURE 6** Diets of three different size-classes (defined by standard length [SL]) Redeye Bass at two locations (Middle Fork Cosumnes River at Rocky Bar and main-stem Cosumnes at Highway 16 [H16]) based on stable isotope mixing models. Prey categories differed across sites due to overlap in isotope values. For example, at main-stem Cosumnes River at H16, Hemiptera and Trichoptera had isotopic values that were indistinguishable from each other, resulting in uncertainty as to which prey item was consumed; therefore, they were condensed into one prey category. Prey category stable isotope values are provided in Table A.3. Results are shown for three size-classes (mm standard length [SL]) of Redeye Bass.



**FIGURE 7** Relative trophic position of three species of fish (Brown Trout *Salmo trutta*, Rainbow Trout, Sacramento Pikeminnow) at three sites where Redeye Bass were present. Relative trophic position represents the trophic level relative to the lowest trophic level of fish present at that site (e.g., primary consumer [relative trophic level = 0] is the lowest trophic level for fish at a site). M. Fork, Middle Fork Cosumnes River; Hwy, Highway.

range in relative trophic positions occupied by fish smaller than 100 mm SL in the Middle Fork Cosumnes River.

### Stable isotope biplots

Biplots of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicated that at sites where Redeye Bass dominated (main-stem Cosumnes River at Latrobe; Middle Fork Cosumnes River), they generally occupied the range of isotopic niche space of all fishes in all sampled reaches (Figure 8). This suggests that Redeye Bass occupied trophic space that was once occupied by native fishes throughout the river.

For comparison, we plotted values for native fishes in one of the few refuges where Redeye Bass are absent (Camp Creek at Happy Valley). The assemblage of Rainbow Trout, California Roach, and Sacramento Sucker exhibited a similar range of isotopic values as the Redeye Bass (Figure 8).

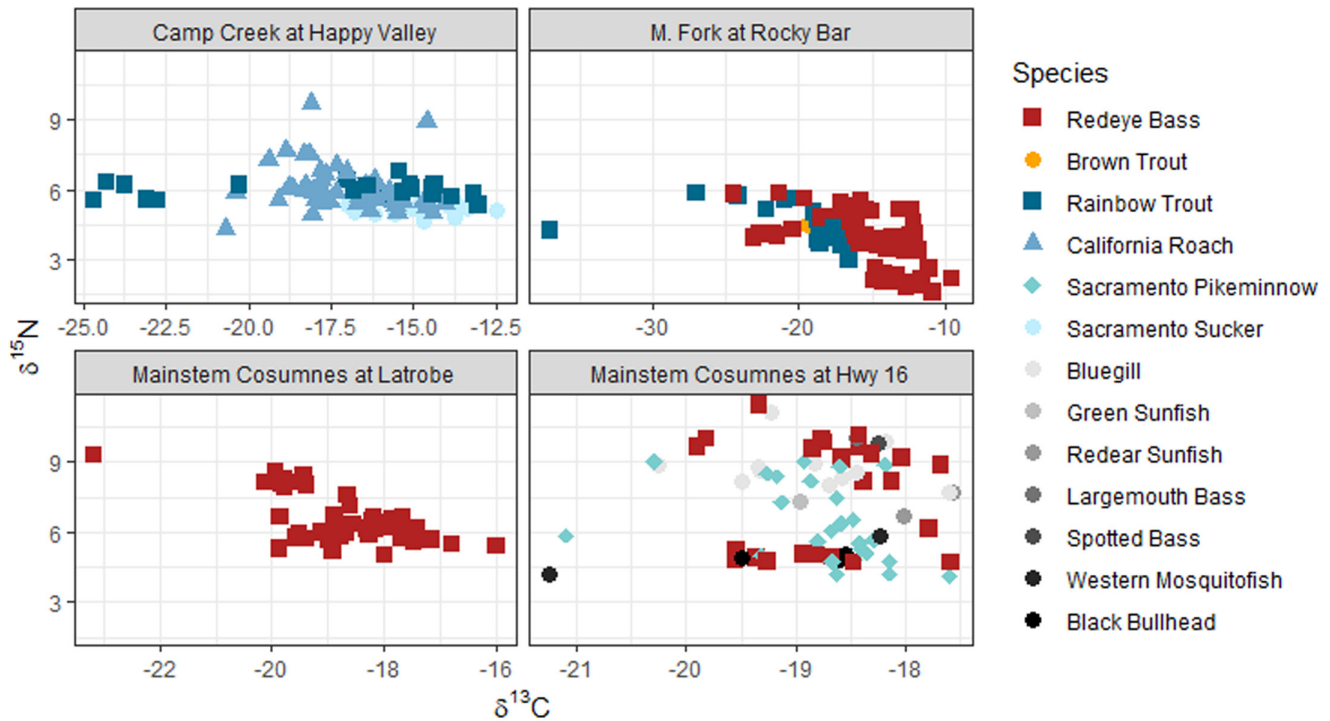
Where Redeye Bass co-occurred with other fish species at the bottom and top limits of their range, the Redeye Bass typically exhibited a wider range of  $\delta^{15}\text{N}$  values than the other sampled species (Figure 8). This indicated that Redeye Bass occupied all trophic niches from primary consumer to top consumer. Notably, individuals from some species (native Sacramento Pikeminnow and Rainbow Trout) exhibited lower  $\delta^{13}\text{C}$  values than Redeye Bass at sites where they overlapped (Figure 8). Despite Redeye Bass being the most

widely distributed nonnative species and often the most common species where they were found, these data suggest that there are still carbon sources in Cosumnes River food webs that may not be consumed by Redeye Bass. In the upper site, isotope values and stomach analysis suggested that these carbon sources were terrestrial (i.e., spiders and adult flies), which were more important in Rainbow Trout diets than in Redeye Bass diets.

## DISCUSSION

### Do Redeye Bass show age and growth patterns similar to those in their native range, or has release from constraints allowed them to grow faster and larger?

Although there are very little growth data available for younger ages of Redeye Bass from their native range, there is no evidence for increased growth or size of Redeye Bass in the Cosumnes River relative to the native range. This is consistent with other analyses documenting general consistency in growth between native and invasive populations of freshwater fish species (Rypel 2014). Slower observed growth and smaller sizes at age in higher elevation locations are also consistent with Rypel (2014), who noted that climate is a crucial factor controlling relative



**FIGURE 8** Biplot of fish stable isotope values (‰; carbon expressed as  $\delta^{13}\text{C}$ ; nitrogen expressed as  $\delta^{15}\text{N}$ ) at locations reflecting four conditions: Redeye Bass absent (Camp Creek at Happy Valley, a tributary to the North Fork Cosumnes River), Redeye Bass co-occurring with trout in the upper watershed at the upper limit of their range (Middle Fork Cosumnes River at Rocky Bar), Redeye Bass dominating the fish community in most of the watershed (main-stem Cosumnes River at Latrobe, in the foothills), and Redeye Bass in the lower watershed at the lower end of their range embedded within a community of other native and nonnative fish species (main-stem Cosumnes River at Highway 16, on the valley floor). Redeye Bass are indicated by red squares, nonnative Brown Trout are indicated by orange circles, native fishes (Rainbow Trout, California Roach, Sacramento Pikeminnow, Sacramento Sucker) are indicated by differently shaped blue points, and other nonnative species (Bluegill *Lepomis macrochirus*, Green Sunfish *L. cyanellus*, Redear Sunfish *L. microlophus*, Largemouth Bass, Spotted Bass, Western Mosquitofish *Gambusia affinis*, Black Bullhead *Ameiurus melas*) are indicated by gray to black circles. M. Fork, Middle Fork Cosumnes River; Hwy, Highway.

growth between different invasive and native populations of the same species. It is possible that elevated growth and greater lengths at age may have been experienced in the first years after the invasion; however, any such growth advantage is no longer evident because the fish community changed dramatically after the introduction of Redeye Bass and other species.

### How does the trophic ecology of Redeye Bass compare to that of the native fishes?

Redeye Bass occupy much of the range of trophic levels that were once occupied by four native fish species that are still found in other parts of the watershed: Sacramento Sucker, California Roach, Rainbow Trout, and Sacramento Pikeminnow. The trophic position of Redeye Bass is most similar to that of the Sacramento Pikeminnow. Sacramento Pikeminnow also prey on fish and macroinvertebrates at adult sizes and consume aquatic invertebrates as juveniles, with prey size increasing with fish

length (Moyle 2002). It is notable that red swamp crayfish constituted nearly 90% of the diet by weight for adult (>113 mm SL) Redeye Bass. The crayfish are also not native, and they are important prey for nonnative fishes throughout California (Moyle 2002).

Although they can be described as generalist and opportunistic predators, Redeye Bass display particular patterns of feeding across ontogeny that are consistent with the patterns shown by other *Micropterus* spp., particularly those that favor lotic environments (e.g., Shoal Bass *M. cataractae* and Guadalupe Bass *M. treculii*). For example, Shoal Bass consume higher proportions of riverine insects than Largemouth Bass in the same area (Wheeler and Allen 2003), with a transition to reliance on crayfish and fish at larger sizes. At a few sites in the lower Cosumnes River, Redeye Bass co-occurred with low numbers of Smallmouth, Largemouth, and Spotted bass. The Redeye Bass was the most abundant species of *Micropterus*. Many *Micropterus* spp. are typically the dominant piscivores in their respective communities, and Redeye Bass in the Cosumnes River are no exception.

Fish contributed minimally to the stomach contents of Redeye Bass (fish prey were found in 2 of 240 stomachs examined), presumably because other fish species were rare at sites where Redeye Bass were abundant (Moyle et al. 2003). Piscivory likely plays a much greater role in structuring the food web than it might seem from these diet data, given seasonality in the availability of fish prey items (i.e., larval fish would be more available when native fishes spawn earlier in the year). Furthermore, visual stomach content analysis can under-report piscivory rates, particularly for predation on larval and juvenile fish (Carreon-Martinez et al. 2011; Brandl et al. 2021). Although we found no evidence of cannibalism, small Redeye Bass would seem to be ready prey for the larger bass, and this may be the reason for the strong habitat segregation by size-class that we observed while snorkeling the river. The nonnative red swamp crayfish provides an abundant prey base for adult Redeye Bass, thus perhaps reducing the energetic necessity of cannibalism.

The trophic impact of Redeye Bass on the native fish community is high for several reasons. First, there are documented changes to fish communities in areas of the Cosumnes River where Redeye Bass are abundant, likely as an aftereffect of predation during the invasion (Moyle et al. 2003). Second, the decline of native species in these reaches reduces their frequency in the diets of predators such as Redeye Bass, but the overall effect of these predators on native fishes is still high (phantom predation; Nobriga and Smith 2020). Third, juvenile Redeye Bass are notably aggressive, which we observed. This behavior may result in juveniles of native fishes being forced out of shallow water and other predation refuges, making native fishes more vulnerable to predation by adult bass. Fourth, aggressive behavior by Redeye Bass may result in exclusion of juvenile native fishes from the forage areas that they need for growth and survival.

There is little hard observational evidence of Redeye Bass predation on native fishes, so we must rely on what observations of California fish populations indicate; if native fishes are absent from a waterway, predation by nonnative fishes is often the most likely cause. Most stream-dwelling native fishes gradually disappear after nonnatives invade their habitats, with a few exceptions. In streams where native fishes prevail, persistence is generally due to the Mediterranean climate flow regimes to which the native fishes are adapted.

### **Do Redeye Bass present a continuing threat to native fishes?**

Redeye Bass have proven to be well suited to thrive in the same environmental conditions that are optimal

for the assemblage of low- to mid-elevation fishes that are native to the Sacramento–San Joaquin River basin (Moyle 2002). Aside from the Cosumnes River, there are eight other major tributaries in California that flow into the Sacramento–San Joaquin River basin in which Redeye Bass introduction would pose a threat to native fishes. Most native fishes appeared to be excluded by Redeye Bass from the Cosumnes River, with the possible exception of Pacific Lamprey. Where Redeye Bass were abundant, native soft-rayed fishes (Sacramento Pikeminnow, California Roach, Sacramento Sucker, Sacramento Speckled Dace, Hardhead, and Rainbow Trout) were absent or rare (Moyle et al. 2003; Chasnoff 2005). The Sacramento Pikeminnow is the principal native piscivore of central California streams with life history and feeding most similar to Redeye Bass. The native fish species occur today mainly above natural barriers that prevent further movement of Redeye Bass in the upper watershed, and native fish species also occur in small numbers in the habitat immediately below these small refuge reaches.

Overall, Redeye Bass have monopolized the trophic and spatial resources of the Cosumnes River at the expense of native fishes. While other species of nonnative fishes are present in the lowermost section of the Cosumnes River (including congeners Smallmouth Bass, Largemouth Bass, and Spotted Bass), they have failed to invade the rest of the river like the Redeye Bass, presumably because of the long, high-gradient section of stream known as Latrobe Falls. Other nonnative fishes also seem to lack adaptations to survive in the colder, smaller creeks higher in the watershed. This pattern is similar to what has happened in the Santa Margarita River, in southern California. Historically, the dominant fish in the stream was the Arroyo Chub *Gila orcutti*, but this species has been largely absent from much of the river since the introduction of Redeye Bass (Moyle 2002).

The nearly complete dominance of the middle reaches of the Cosumnes River by Redeye Bass is surprising. Given that the Redeye Bass is endemic to a relatively small region, though with a diverse fish assemblage, in the southeastern United States, it might be expected that it would be too specialized to be moved to a region that is climatically so different. The Redeye Bass was chosen for introduction because it was thought to be an attractive game fish adapted for small streams (Moyle 2002). We hypothesize that the success of Redeye Bass is due to the following combination of factors:

- Adaptations that allow them to survive in colder, smaller creeks higher in the watershed than other *Micropterus* spp.

- The presence of numerous deep bedrock pools that serve as late-summer, low-flow refuges, as shown by microhabitat use.
- Like some other *Micropterus* spp., Redeye Bass exhibit aggressive behavior that allows them to dominate the system. They can displace fishes even in the absence of direct predation, show little fear of people snorkeling in the pools, and are brightly colored and conspicuous.
- Small sized as adults, which enables them to be abundant in a small stream.
- Morphology as a generalized predator and propensity for opportunistic feeding, enabling them to feed at all trophic levels.
- Absence of other bass species in the middle watershed, such as Smallmouth and Largemouth bass, which may prey on the much smaller Redeye Bass.

The Redeye Bass invasion is a good example of the principle espoused by Moyle and Light (1996) that under the right circumstances, any fish species can be an invader and any aquatic habitat can be invaded. Redeye Bass are notably doing well in an unregulated river despite the variability in flows created by the Californian climate, which is typically unfavorable to nonnative species. Lack of data limits our understanding of the effects of hydrology on Redeye Bass populations, which is essential for managing for native fish conservation. California native species are adapted to thrive in prolonged seasonal droughts that are typical of summer and fall. The Cosumnes River flow regime is defined by erratic peak winter/spring flows and low summer/fall flows in contrast to the less variable river flow regimes and wetter climate of the southeastern United States.

Curiously, Redeye Bass appear to be slow dispersers from either the Cosumnes River or the nearby Stanislaus River into other river systems in California. Despite a long history in the two watersheds, they are rarely encountered in downstream habitats. For example, it is remarkable that Redeye Bass were not encountered during 5 years of intensive sampling of fishes using the Cosumnes River floodplain (Moyle et al. 2007). Clause et al. (2023) also documented that the occurrence of Redeye Bass further downstream in tidal sloughs is rare.

Nevertheless, because of frequent confusion with Smallmouth Bass over the past 50 years, Redeye Bass are likely more widespread in California than is known (Moyle 2002; Valente et al. 2021). If Redeye Bass are found or introduced into additional waterways, proactive management would be necessary to protect threatened endemic fish and invertebrates. Management options are limited once Redeye Bass become established in a river. Options for management include providing refuges for native fishes, preventing colonization of new waters (e.g.,

construction of barriers), and opportunistic eradication programs when populations are naturally low or have restricted distributions due to drought or other factors. The limited options for dealing with this successful invasion remind us once again of the need to prevent the introduction of nonnative species or suffer the unintended consequences of these invasions.

## ACKNOWLEDGMENTS

This research was supported by the Ecosystem Restoration Program of the CALFED Bay-Delta Program (99-NO6 and 99-B193). Stellar field assistance was provided by Karl Osmundson, Teryn Kravitz, Jesse Morgan Castle, and Joseph Sullivan. Jake Vander Zanden, Collin Eagles-Smith, and David Harris helped with stable isotope analyses. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the lead author Beth Long ([bethchas@gmail.com](mailto:bethchas@gmail.com)) upon reasonable request.

## ETHICS STATEMENT

All fish were collected under the guidelines of Protocol 48883 approved by the Institutional Animal Care and Use Committee at the University of California, Davis. Collections were authorized under Scientific Collection Permit 001928 issued by the California Department of Fish and Wildlife.

## ORCID

Beth Chasnoff  <https://orcid.org/0009-0003-0117-9858>

Peter B. Moyle  <https://orcid.org/0000-0002-4825-4865>

Matthew J. Young  <https://orcid.org/0000-0001-9306-6866>

## REFERENCES

- Baker, W. H., Blanton, R. E., & Johnston, C. E. (2013). Diversity within the Redeye Bass, *Micropterus coosae* (Perciformes: Centrarchidae) species group, with descriptions of four new species. *Zootaxa*, 3635(4), 379–401. <https://doi.org/10.11646/zootaxa.3635.4.3>
- Baltz, D. M., & Moyle, P. B. (1993). Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications*, 3, 246–255. <https://doi.org/10.2307/1941827>
- Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern

- United States. *Journal of the North American Benthological Society*, 18, 308–343. <https://doi.org/10.2307/1468447>
- Bonar, S. A., Hubert, W. A., & Willis, D. W. (Eds.). (2009). *Standard methods for sampling North American freshwater fishes*. American Fisheries Society.
- Brandl, S., Schreier, B., Conrad, J. L., May, B., & Baerwald, M. (2021). Enumerating predation on Chinook Salmon, Delta Smelt, and other San Francisco Estuary fishes using genetics. *North American Journal of Fisheries Management*, 41(4), 1053–1065. <https://doi.org/10.1002/nafm.10582>
- Cabana, G., & Rasmussen, J. B. (1996). Comparison of aquatic food chains using stable nitrogen isotopes. *Proceedings of the National Academy of Sciences of the United States of America*, 93, 10844–10847. <https://doi.org/10.1073/pnas.93.20.10844>
- Carreon-Martinez, L., Johnson, T. B., Ludsin, S. A., & Heath, D. D. (2011). Utilization of stomach content DNA to determine diet diversity in piscivorous fishes. *Journal of Fish Biology*, 78, 1170–1182. <https://doi.org/10.1111/j.1095-8649.2011.02925.x>
- Chasnoff, B. (2005). *Food webs in the Cosumnes River* [Doctoral dissertation, University of California, Davis].
- Clause, J. K., Young, M. J., Huntsman, B. M., Perry, R. W., Pope, A. C., & Feyrer, F. V. (2023). *Distribution and stomach contents of fishes in the northern Sacramento-San Joaquin Delta, 2020-2022* [Data release]. U.S. Geological Survey. <https://doi.org/10.5066/P9LN77LW>
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., et al. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81, 163–182. <https://doi.org/10.1017/S1464793105006950>
- Fritts, A. L., & Pearsons, T. N. (2006). Effects of predation by non-native Smallmouth Bass on native salmonid prey: The role of predator and prey size. *Transactions of the American Fisheries Society*, 135, 853–860. <https://doi.org/10.1577/T05-014.1>
- Gu, B. H., Schell, D. M., & Alexander, V. (1994). Stable carbon and nitrogen isotopic analysis of the plankton foodweb in a subarctic lake. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 1338–1344. <https://doi.org/10.1139/f94-133>
- Gwinner, H. R. (1973). *A study of the Redeye Bass, Micropterus coosae, Smallmouth Bass, Micropterus dolomieu, and Rockbass, Ambloplites rupestris in Spring Creek, Tennessee* [Master's thesis, Tennessee Technological University].
- Huntsman, B. M., Brown, L. R., Palenscar, K., Jones, C., Russell, H. D., Mills, H., Wulff, M. L., & May, J. (2022). Joint-species analysis reveals potential displacement of native fishes by non-native fishes within the Santa Ana River, California. *Canadian Journal of Fisheries and Aquatic Sciences*, 9, 1389–1406. <https://doi.org/10.1139/cjfas-2021-0210>
- Jacinto, E., Fangué, N. A., Cocherell, D. E., Kiernan, J. D., Moyle, P. B., & Rypel, A. L. (2023). Increasing stability of a native freshwater fish assemblage following flow rehabilitation. *Ecological Applications*, 33, Article e2868. <https://doi.org/10.1002/eap.2868>
- Jackson, D. A. (2002). Ecological effects of *Micropterus* introductions: The dark side of black bass. In D. P. Philipp & M. S. Ridgway (Eds.), *Black bass: Ecology conservation, and management* (Symposium 31, pp. 221–232). American Fisheries Society.
- Kiernan, J. D., Moyle, P. B., & Crain, P. K. (2012). Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. *Ecological Applications*, 22, 1472–1482. <https://doi.org/10.1890/11-0480.1>
- Kline, T., Jr., Goering, J., Mathisen, O., Poe, P., Parker, P., & Scalan, R. (1993). Recycling of elements transported upstream by runs of Pacific salmon: II.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 50(11), 2350–2365. <https://doi.org/10.1139/f93-259>
- Kling, G. W., Fry, B., & O'Brien, W. J. (1992). Stable isotopes and planktonic trophic structure in arctic lakes. *Ecology*, 73, 561–566. <https://doi.org/10.2307/1940762>
- Leidy, R. A., & Moyle, P. B. (1997). Conservation status of the world's fish fauna: An overview. In P. A. Fiedler & P. M. Karieva (Eds.), *Conservation biology for the coming decade* (pp. 187–227). Chapman and Hall.
- Leidy, R. A., & Moyle, P. B. (2021). Keeping up with the status of freshwater fishes: A California (USA) perspective. *Conservation Science and Practice*, 3(8), Article e474. <https://doi.org/10.1111/csp2.474>
- Leitner, J. K., & Earley, L. A. (2015). Redeye bass *Micropterus coosae*, Hubbs and Bailey 1940. In M. D. Tringali, J. M. Long, T. W. Birdsong, & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation* (Symposium 82, pp. 61–66). American Fisheries Society. <https://doi.org/10.47886/9781934874400.ch7>
- Lever, C. (1996). *Naturalized fishes of the World*. Academic Press.
- Light, T., & Marchetti, M. P. (2007). Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology*, 21, 434–446. <https://doi.org/10.1111/j.1523-1739.2006.00643.x>
- Light, T., & Moyle, P. B. (2015). Assembly rules and novel assemblages in aquatic ecosystems. In J. Canning-Clode (Ed.), *Biological invasions in changing ecosystems: Vectors, ecological impacts, management, and predictions* (pp. 432–457). De Gruyter Open. <https://doi.org/10.1515/978310438666-026>
- Marchetti, M. P., & Moyle, P. B. (2001). Effects of flow regime on fish assemblages in a regulated California stream. *Ecological Applications*, 11, 530–539. [https://doi.org/10.1890/1051-0761\(2001\)011\[0530:EOFROF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0530:EOFROF]2.0.CO;2)
- McCutchan, J. H., Lewis, W. M., Kendall, C., & McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, 102(2), 378–390. <https://doi.org/10.1034/j.1600-0706.2003.12098.x>
- Moore, J. W., & Semmens, B. X. (2008). Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters*, 11, 470–480. <https://doi.org/10.1111/j.1461-0248.2008.01163.x>
- Moyle, P. B. (2002). *Inland fishes of California: Revised and updated*. University of California Press.
- Moyle, P. B., & Baltz, D. M. (1985). Microhabitat use by an assemblage of California stream fishes: Developing criteria for in-stream flow determinations. *Transactions of the American Fisheries Society*, 114, 695–704. [https://doi.org/10.1577/1548-8659\(1985\)114<695:MUBAAO>2.0.CO;2](https://doi.org/10.1577/1548-8659(1985)114<695:MUBAAO>2.0.CO;2)
- Moyle, P. B., Crain, P. K., & Whitener, K. (2007). Patterns in the use of a restored California floodplain by native and alien fishes. *San Francisco Estuary and Watershed Science*. *Science*, 5(3), Article 1. <https://doi.org/10.1544/sfews.2007v5iss5art1>

- Moyle, P. B., Crain, P. K., Whitener, K., & Mount, J. F. (2003). Alien fishes in natural streams: Fish distribution, assemblage structure, and conservation in the Cosumnes River, California, USA. *Environmental Biology of Fishes*, 68, 143–162. <https://doi.org/10.1023/B:EBFI.0000003846.54826.a6>
- Moyle, P. B., Katz, J. V., & Quinones, R. M. (2011). Rapid decline of California's native inland fishes: A status assessment. *Biological Conservation*, 144(10), 2414–2423. <https://doi.org/10.1016/j.biocon.2011.06.002>
- Moyle, P. B., & Leidy, R. A. (2023). Freshwater fishes: Threatened species and threatened waters on a global scale. In N. Maclean (Ed.), *The living planet: The present state of the world's wildlife* (pp. 177–206). Cambridge University Press.
- Moyle, P. B., & Light, T. (1996). Fish invasions in California: Do abiotic factors determine success? *Ecology*, 77, 1666–1670. <https://doi.org/10.2307/2265770>
- Moyle, P. B., & Marchetti, M. P. (2006). Predicting invasion success: Freshwater fishes in California as a model. *Bioscience*, 56, 515–524. [https://doi.org/10.1641/0006-3568\(2006\)56\[515:PISFFI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[515:PISFFI]2.0.CO;2)
- Moyle, P. B., Quinones, R. M., Katz, J. V. E., & Weaver, J. (2015). *Fish species of special concern in California* (3rd ed.). California Department of Fish and Wildlife. <https://wildlife.ca.gov/Conservation/Fishes/Dpecial-Concern>
- Nobriga, M. L., Michel, C. J., Johnson, R. C., & Wikert, J. D. (2021). Coldwater fish in a warm water world: Implications for predation of salmon smolts during estuary transit. *Ecology and Evolution*, 11(15), 10381–10395. <https://doi.org/10.1002/ece3.7840>
- Nobriga, M. L., & Smith, W. E. (2020). Did a shifting ecological baseline mask the predatory effect of Striped Bass on Delta Smelt? *San Francisco Estuary and Watershed Science*, 18(1), Article 1. <https://doi.org/10.15447/sfews.2020v18iss1art1>
- Page, L. M., Bemis, K. E., Dowling, T. E., Espinosa-Pérez, H. S., Findley, L. T., Gilbert, C. R., Hartel, K. E., Lea, R. N., Mandrak, N. E., Neighbors, M. A., Schmitter-Soto, J. J. & Walker, H. J. (2023). *Common and scientific names of fishes from the United States, Canada, and Mexico* (8th ed., Special Publication 37). American Fisheries Society. <https://doi.org/10.47886/9781934874691>
- Parsons, J. W. (1954). Growth and habits of the Redeye Bass. *Transactions of the American Fisheries Society*, 83, 202–211. [https://doi.org/10.1577/1548-8659\(1953\)83\[202:GAHOTR\]2.0.CO;2](https://doi.org/10.1577/1548-8659(1953)83[202:GAHOTR]2.0.CO;2)
- Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., Semmens, B. X., & Ward, E. J. (2014). Best practices for use of stable isotope mixing models in food web studies. *Canadian Journal of Zoology*, 92(10), 823–835. <https://doi.org/10.1139/cjz-2014-0127>
- Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83, 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)
- R Core Team. (2002). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3), 849–873. <https://doi.org/10.1111/brv.12480>
- Rypel, A. L. (2014). Do invasive freshwater fish species grow better when they are invasive? *OIKOS*, 123(3), 279–289. <https://doi.org/10.1111/j.1600-0706.2013.00530.x>
- Sabo, J. L., Bastow, J. L., & Power, M. E. (2002). Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society*, 21(2), 336–343. <https://doi.org/10.2307/1468420>
- Stock, B. C., & Semmens, B. X. (2016). MixSIAR GUI user manual (Ver. 3.0).
- Takamura, K. (2007). Performance as a fish predator of Largemouth Bass [*Micropterus salmoides* (Lacepède)] invading Japanese freshwaters: A review. *Ecological Research*, 22, 940–946. <https://doi.org/10.1007/s11284-007-0415-7>
- Valente, M. J., Benson, C. E., Chmiel, M. R., Lewis, M. R., Peatmann, E., & Eaton, H. L. (2021). A case of mistaken identity: Genetic and morphological evidence for the presence of Redeye Bass in the Verde River, Arizona. *Journal of Fish and Wildlife Management*, 12(2), 554–564. <https://doi.org/10.3996/JFWM-21-013>
- Ward, G. M., Ward, A. L., & Harris, P. M. (2023). Gulf Coast rivers of the southeast United States. In M. D. DeLong, T. D. Jardine, A. C. Benke, & C. E. Cushing (Eds.), *Rivers of North America* (2nd ed., pp. 124–175). Academic Press.
- Weinersmith, K. L., Colombano, D. D., Bibian, A. J., Young, M. J., Sih, A., & Conrad, J. L. (2019). Diets of Largemouth Bass (*Micropterus salmoides*) in the Sacramento San Joaquin Delta. *San Francisco Estuary and Watershed Science*, 17(1), Article 3. <https://doi.org/10.15447/sfews.2019v17iss1art3>
- Wheeler, A. P., & Allen, M. S. (2003). Habitat and diet partitioning between Shoal Bass and Largemouth Bass in the Chipola River, Florida. *Transactions of the American Fisheries Society*, 132(3), 438–449. [https://doi.org/10.1577/1548-8659\(2003\)132\[0438:HADPBS\]2.0.CO;2](https://doi.org/10.1577/1548-8659(2003)132[0438:HADPBS]2.0.CO;2)
- Woodford, D. J., Impson, N. D., Day, J. A., & Bills, I. R. (2005). The predatory impact of invasive alien Smallmouth Bass, *Micropterus dolomieu* (Teleostei: Centrarchidae), on indigenous fishes in a Cape Floristic Region mountain stream. *African Journal of Aquatic Science*, 30, 167–173. <https://doi.org/10.2989/16085910509503852>
- Wright, S. E. (1967). Life history and taxonomy of the Flint River Redeye Bass (*Micropterus coosae*, Hubbs and Bailey) [Unpublished doctoral dissertation]. University of Georgia.

## SUPPORTING INFORMATION

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

## APPENDIX

## Fishes of the Cosumnes River.

TABLE A.1 Fishes collected at 32 sampling sites in the Cosumnes River basin, California. Native species are marked in bold.

Species	Sites	Occurrence <sup>a</sup>
American Shad <i>Alosa sapidissima</i>	1	M
White Catfish <i>Ameiurus catus</i>	2	M
Black Bullhead <i>Ameiurus melas</i>	3	M
<b>Sacramento Sucker <i>Catostomus occidentalis</i></b>	5	NF&T, M
<b>Prickly Sculpin <i>Cottus asper</i></b>	3	M&T
Western Mosquitofish <i>Gambusia affinis</i>	7	NF H, SF, M&T
<b>Pacific Lamprey <i>Entosphenus tridentatus</i></b>	7	MF, NF, M
Green Sunfish <i>Lepomis cyanellus</i>	8	SF, M&T
Bluegill <i>L. macrochirus</i>	7	M&T
Redear Sunfish <i>L. microlophus</i>	4	SF, M
<b>California Roach <i>Hesperoleucus symmetricus</i></b>	7	NF&T, SF&T, D
Redeye Bass <i>Micropterus coosae</i>	10	MF, M
Smallmouth Bass <i>Micropterus dolomieu</i>	2	M
Spotted Bass <i>Micropterus punctulatus</i>	2	M
Largemouth Bass <i>Micropterus nigricans</i>	1	M
Striped Bass <i>Morone saxatilis</i>	1	M
<b>Rainbow Trout <i>Oncorhynchus mykiss</i></b>	16	MF&T, NF&T, SF
Bigscale Logperch <i>Percina macrolepida</i>	1	M
<b>Sacramento Pikeminnow <i>Ptychocheilus grandis</i></b>	5	M&T
Brown Trout <i>Salmo trutta</i>	8	MF&T, NF&T, SF
Brook Trout <i>Salvelinus fontinalis</i>	1	NF H

<sup>a</sup> Occurrence codes: D, Deer Creek (a tributary of the main stem); H, headwaters; M, main-stem Cosumnes River; MF, Middle Fork Cosumnes River; NF, North Fork Cosumnes River; SF, South Fork Cosumnes River; T, tributary.

TABLE A.2 Number of individuals (#), mass (mg), and percentage (%) of total mass of prey items found in the stomach contents of Redeye Bass. The Redeye Bass were divided into three size-classes: class 1 (&lt;61 mm standard length [SL]), class 2 (61–113 mm SL), and class 3 (&gt;113 mm SL).

Prey group	Taxon or stage	Size-class 1 (n = 77)			Size-class 2 (n = 87)			Size-class 3 (n = 76)		
		#	Mass	%	#	Mass	%	#	Mass	%
Amphipoda		27	1.2	<1	0	0	0	0	0	0
Coleoptera	Larvae	5	2.1	<1	22	55.6	2	7	23.5	<1
	Adults	3	1.2	<1	0	0	0	1	4.6	<1
Decapoda		1	33	7	4	2195	77	5	33,778	88
Diptera	Chironomidae larvae	158	7.2	2	72	2.8	<1	4	1.7	<1
	Simuliidae larvae	21	3.9	1	83	20.6	1	86	38.3	<1
	Other larvae/pupae	4	<0.1	<1	2	2.9	<1	2	4.5	<1
Ephemeroptera	Adults	4	<0.1	<1	5	0.1	<1	1	0.2	<1
	Larvae	254	305	64	264	109	4	31	478	1
	Adult	4	0.3	<1	2	0.1	<1	0	0	0

TABLE A.2 (Continued)

Prey group	Taxon or stage	Size-class 1 (n = 77)			Size-class 2 (n = 87)			Size-class 3 (n = 76)		
		#	Mass	%	#	Mass	%	#	Mass	%
Hemiptera		6	4.1	1	3	5.2	<1	4	8.3	<1
Lepidoptera	Larvae	15	18.3	4	23	21	1	0	0	0
Megaloptera	Larvae	2	15.6	3	3	18.3	1	13	2979	8
Mollusca	Gastropoda	0	0	0	1	0.8	<1	0	0	0
	Bivalvia	0	0	0	0	0	0	2	5.5	<1
Odonata	Anisoptera larvae	41	20.1	4	34	169	6	3	59.9	<1
	Zygoptera larvae	7	12.8	3	7	35.6	1	3	836	2
Oligochaetes		0	0	0	2	NA	NA	0	0	0
Plecoptera	Larvae	7	9.6	2	15	53.8	2	5	52.5	<1
Terrestrial	Arachnida	0	0	0	4	21.1	1	0	0	0
	Hymenoptera	3	12.4	3	0	0	0	0	0	0
	Dermoptera	0	0	0	3	80.0	3	0	0	0
	Other	2	4.4	1	1	6.5	<1	1	1.8	<1
Trichoptera	Hydropsychidae larvae	0	0	0	6	16.3	1	19	42.0	<1
	Other larvae	102	27.6	6	51	33.4	1	15	24.9	<1
	Adults	12	0.2	<1	4	1.0	<1	0	0	0
Ranidae	Eggs	12	NA	NA	0	0	0	0	0	0
Other fish		0	0	0	0	0	0	2	NA	NA
Total		690	480	100	611	2847	100	204	38,338	100

TABLE A.3 Stable isotope values (‰) of prey categories used for mixing model input. Values are presented as mean and standard deviation (SD).

Site	Prey category	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		Mean	SD	Mean	SD
Main-stem Cosumnes River at Highway 16	Hemiptera/Trichoptera	-17.57	0.9	2.88	0.7
	Odonata	-17.59	0.7	4.39	0.3
	Plecoptera/Decapoda	-19.22	0.8	4.03	0.8
	Fish	-19.10	1.5	5.25	1.4
Middle Fork Cosumnes River at Rocky Bar	Diptera	-14.98	0.9	0.38	0.1
	Trichoptera/Odonata	-15.78	0.7	1.72	0.3
	Odonata/Plecoptera	-21.32	2.1	2.65	0.3
	Plecoptera	-24.72	3.0	0.85	0.7
	Decapoda/fish	-18.33	2.3	2.80	1.0