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# SPATIAL, SEASONAL, AND SIZE-DEPENDENT VARIATION IN THE DIET OF SACRAMENTO PIKEMINNOW IN THE EEL RIVER, NORTHWESTERN CALIFORNIA

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**We examined the food habits of 2,077 Sacramento pikeminnow (46-550 mm standard length [SL]) collected from the mainstem Eel River and South Fork Eel River, California in 1995 - 1997. Fifty-eight percent of the fish contained prey in the upper digestive tract. Sacramento pikeminnow consumed a wide variety of prey; the diversity of individual diets was higher from February - May compared to July - October and higher in the South Fork Eel River than in the mainstem Eel River. The proportion of fish in the diet increased with Sacramento pikeminnow length but diet diversity did not. Sacramento pikeminnow collected from the South Fork Eel River in the late season contained the highest proportion of fish. Predator and prey size were also positively related. In general, Sacramento pikeminnow preyed on lamprey and fishes in proportion to their availability, as estimated by electrofishing collections, but tended to avoid cannibalism. Six percent of the Sacramento pikeminnow containing food in the upper digestive tract had consumed juvenile salmonids. Sacramento pikeminnow were not more abundant where salmonids were present. Predation risk for salmonids may be most significant where the species occur together during low, clear water conditions. For example, 44% of 43 Sacramento pikeminnow > 250 mm SL from our upstream-most collecting site on the South Fork Eel River in August 1995 contained salmonids. In most of our study area, predation risk for outmigrating salmonids may be reduced by high turbidity and the availability of alternative prey. However, strong conclusions about the ability of Sacramento pikeminnow in the Eel River to reduce salmonid populations will require information on food habits when juvenile salmonids are abundant, and population estimates for the predator.**

## INTRODUCTION

Sacramento pikeminnow, *Ptychocheilus grandis*, are native to the Sacramento-San Joaquin drainage and several coastal drainages in northern California (Moyle 2002). Around 1979, Sacramento pikeminnow were illegally introduced into Pillsbury Reservoir, on the upper mainstem Eel River. Within 10 years of their introduction, Sacramento pikeminnow expanded their distribution throughout the mainstem Eel River and most of its tributaries (Brown and Moyle 1997). The predatory nature of Sacramento pikeminnow prompted widespread concern over their potential effect on depressed populations of anadromous salmonids in the Eel River. Brown and Moyle (1997) concluded that Sacramento pikeminnow from the Eel River do not appear to prey on significant numbers of juvenile salmon except under localized conditions. Overall, salmonids made up <10% of the diet of Sacramento pikeminnow collected from the Eel River between 1986 and 1990 (Brown and Moyle 1997). However, the diet of Sacramento pikeminnow was not the primary focus of Brown and Moyle (1997), and that study was limited somewhat by few samples from large Sacramento pikeminnow (> 250 mm standard length [SL]), particularly during the primary period of out-migration by juvenile salmonids. Large individuals are critical to the assessment of Sacramento pikeminnow predation on salmonids because the extent of piscivory increases with body size (Brown 1990, Brown and Moyle 1997). Further, except during their spawning period, large Sacramento pikeminnow are found almost exclusively in the mainstem Eel River and its major tributaries. Thus, as the juvenile salmonids leave low-order channels to begin their seaward migration, they may be exposed to the highest risk of predation from large Sacramento pikeminnow. The goal of this study was to characterize the spatial and seasonal variability in the diet of Sacramento pikeminnow from the Eel River, while incorporating variation attributable to body size.

## STUDY SITE

The Eel River drains a 953,294-ha catchment with four major tributaries: the North, Middle and South forks of the Eel River, and the Van Duzen River (Fig. 1). For logistical reasons, we focused our sampling efforts on the lower mainstem Eel River (MSER), South Fork Eel River (SFER) and the lower Van Duzen River (VDZR). Annual discharges in the MSER, SFER, and VDZR are highly variable and closely tied to precipitation.

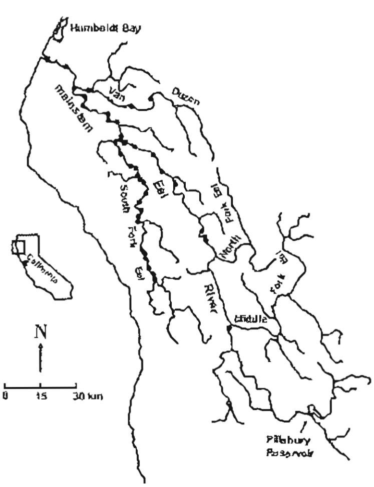


Figure 1. Locations of sampling sites in the Van Duzen River, mainstem Eel River and South Fork Eel River, California.

During hydrologic year 1996, discharge ranged <3 - 11,300 $m^3/s$ in the MSER, <1 - 2650 $m^3/s$ in the SFER and <0.2 - 1028 $m^3/s$ in the VDZR. Water temperatures in the large channels of the Eel drainage commonly exceed 25 °C during summer, rendering much of the Eel River inhospitable to juvenile salmonids. The SFER tends to be slightly cooler than the MSER and VDZR, in part due to greater shading by riparian vegetation and input from cool-water tributaries. The SFER study reach also included mesohabitats with greater structural complexity than those in the MSER and VDZR.

Historically, the Eel River supported six species of anadromous salmonids including coho salmon, *Oncorhynchus kisutch*, chinook salmon, *O. tshawytscha*, pink salmon, *O. gorbuscha*, chum salmon, *O. keta*, steelhead, *O. mykiss*, including resident rainbow trout, and cutthroat trout, *O. clarki*. Chinook salmon, coho salmon, and steelhead are listed as Threatened under the United States Endangered Species Act; and pink and chum salmon have disappeared from the drainage (Brown and Moyle 1997). Other native fishes of the Eel River include Sacramento sucker, *Catostomus occidentalis*, prickly sculpin, *Cottus asper*, coastrange sculpin, *C. aleuticus*, threespine stickleback, *Gasterosteus aculeatus*, and Pacific lamprey, *Lampetra tridentata*. At least 10 introduced fishes have established reproducing populations the Eel River (Brown and Moyle 1997). California roach, *Hesperoleucus* or *Lavinia symmetricus*, and Sacramento pikeminnow are the most widespread of the introduced species and probably the most abundant fish in the Eel River (Brown and Moyle 1997). Speckled dace, *Rhinichthys osculus*, occupy approximately 25 km of the Van Duzen River. American shad, *Alosa sapidissima*, originally introduced into the Sacramento-San Joaquin river system, have strayed into the Eel River. White catfish, *Ameiurus catus*, are present in the mainstem Eel River. Threadfin shad, *Dorosoma petenense*, golden shiner, *Notemigonus crysoleucas*, bluegill, *Lepomis macrochirus*, largemouth bass, *Micropterus salmoides*, brown bullhead, *Ameiurus nebulosus*, green sunfish, *Lepomis cyanellus*, are mainly confined to Pillsbury Reservoir, but occasionally encountered in the MSER and large tributaries.

## METHODS

We established a total of 39 sample stations: 18 in the MSER in the 165-km reach extending upstream from the upper estuary, 18 sample stations in the SFER in the reach extending 104 km upstream from the confluence with the mainstem, and 3 sample stations on the lower VDZR (Fig. 1). We repeatedly sampled fishes at each station between April 1995 and March 1997, primarily with a custom-built electrofishing boat equipped with a Smith-Root model 7.5 GPP electrofishing unit. We usually collected fish between 0600 and 1300 h, using 60 Hz, pulsed direct current. During periods of low river discharge, collections were limited to pools and runs. When higher discharge allowed greater mobility by boat, we sampled extensively in reaches up to 500 m long. Reach length was scaled to reflect diel movements by adult pikeminnow (Harvey and Nakamoto 1999). All stations were sampled at low and high discharge. To reduce the risk of electrofishing injuries to adult anadromous salmon, we did not sample during November, December, and January.

During each sampling run, we held all captured fishes in a water-filled ice chest. We recorded species-specific counts and approximate lengths for fish observed but not captured. Length estimates for these fishes were calibrated with subsequent measurements of captured individuals of the same species. Except for Sacramento pikeminnow, fishes were anesthetized with tricaine methanosulfonate, identified to species, measured, and released. Sacramento pikeminnow were administered a lethal dose of tricaine methanosulfonate prior to processing. Sacramento pikeminnow $\leq$ 150 mm SL were measured and preserved whole in 10% formalin. We perforated the coelomic cavity to improve preservation of gut contents. The entire digestive tract of Sacramento pikeminnow > 150 mm SL was excised and preserved in 70% ethanol. Field processing of samples was completed within 30 min of capture. All gut samples were returned to the laboratory for analysis.

In the laboratory, we retrieved prey items from the esophagus to the second turn of the S-shaped digestive tract. In general, we identified prey taxa to species for vertebrates, family for insects, and order for other invertebrates. Prey were then enumerated, blotted dry, and weighed to the nearest 0.001 g. Following Hansel et al. (1988), we examined the morphology and length of cleithra and pharyngeal arches from known fishes to identify well-digested fish and estimate fish length. Our data yielded strong species-specific regressions (all $r^2 > 0.97$) that predicted prey standard length using cleithrum length or pharyngeal arch length.

Diet data were categorized by river and season for analyses. We grouped data from the VDZR and MSER based on their relatively similar physical characteristics and the rarity of salmonids in those reaches during summer. We defined February to May, when juvenile salmonids are most abundant in main channels of the drainage, as the "Early" season, and samples collected from June to October as the "Late" season. By the beginning of the late season most juvenile salmonids in the large channels we sampled have migrated to the ocean and any that remain in the drainage are primarily limited to cool water tributaries (Brown and Moyle 1997, Harvey et al. 2002).

We summarized and analyzed overall patterns in Sacramento pikeminnow food habits in several ways. First, we divided prey into three broad categories: fishes (including Pacific lamprey), insects, and miscellaneous, then calculated the proportion (by weight) of each category in the diet by river and predator size. We also summarized diet composition in greater taxonomic detail by river, season, and two categories of Sacramento pikeminnow size ($\leq$ 250 mm SL, > 250 mm SL). We analyzed overall patterns in Sacramento pikeminnow diet using the Shannon-Wiener diversity index (H′) as a response variable, where $H' = -\Sigma p_i \ln p_i$. We calculated the proportional composition of individual Sacramento pikeminnow diets ($p_i$'s) using both the mass and the number of individuals in each taxonomic category. We analyzed H′ using analysis of covariance (ANCOVA), with river and season as main effects and Sacramento pikeminnow standard length as the covariate.

We analyzed piscivory by Sacramento pikeminnow in greater detail, because of its potential significance to resource managers. First, we analyzed the proportion of fish (by weight) in the diet using the same ANCOVA design used to evaluate diet diversity. Second, we quantified the relationship between Sacramento pikeminnow size and fish prey size using linear regression. Third, we sought to quantify the degree of selection by Sacramento pikeminnow for specific fishes or lamprey by using our estimates of prey availability to compute electivity. We used the electivity index $L_i = r_i - p_i$ (Strauss 1979) where $r_i$ is the relative abundance of taxon *i* in the fish component of the Sacramento pikeminnow diet and $p_i$ is the relative abundance of the $i^{th}$ taxon in the river. We limited this analysis to Sacramento pikeminnow > 250 mm SL to focus on highly piscivorous individuals. Fish < 163 mm SL were considered potential prey, reflecting the maximum size of fish prey in the dataset. All Pacific lamprey were included as potential prey, because we captured a Sacramento pikeminnow 470 mm SL during this study that had consumed a Pacific lamprey 600 mm total length. We included in this analysis the seven vertebrates commonly observed both during sampling and in the diet. Due to difficulties in distinguishing species during electrofishing when fish evaded capture and in well-digested diet samples, we grouped steelhead, chinook salmon, and coho salmon as *Oncorhynchus* spp. and coast range and prickly sculpins as *Cottus* spp. Electivities were calculated for each combination of sampling location and date. We analyzed the effects of river and season on electivity with ANOVA. We also used *t*-tests to identify electivity values significantly different from 0. We adjusted the probability levels of individual *t*-tests to achieve an experimentwise significance level of 0.05. One obvious weakness of this analysis of prey selection is the bias in the prey availability data caused by species-specific differences in the probability of observation and changes in our ability to detect fish under varying physical conditions. Finally, to determine if Sacramento pikeminnow were more abundant where salmonids were present, we used catch-per-unit-effort data to contrast densities of Sacramento pikeminnow > 250 mm SL at sample sites with and without salmonids using a *t*-test. Sites where we observed salmonids during electrofishing or where at least one Sacramento pikeminnow contained salmonids were categorized as sites with salmonids present. We limited this analysis to the early season because salmonids were seldom encountered during the late season.

## RESULTS

We examined the gut contents of 2,077 Sacramento pikeminnow ranging from 46 - 550 mm SL. For fish collected in the early season, we found prey in 59% of the samples collected from the MSER and 73% of the samples collected from the SFER. During the late season, 55% of the samples collected from the MSER and 41% of the samples from the SFER contained prey.

Overall, invertebrates became less abundant and fish more abundant in the diet with increasing Sacramento pikeminnow size (Fig. 2), and Sacramento pikeminnow consumed a wide variety of prey (Table 1). When grouped by river, season, and Sacramento pikeminnow size, no prey category made up more than one-third of the diet (Table 1). During the early season, in the MSER, Pacific lamprey, Hemiptera, Plecoptera, and Odonata predominated in the diet of small (≤ 250 mm SL) Sacramento pikeminnow (about 10% - 14% each). The diets of small Sacramento pikeminnow from the SFER were similar to the diet of small Sacramento pikeminnow from the MSER in the early season, except

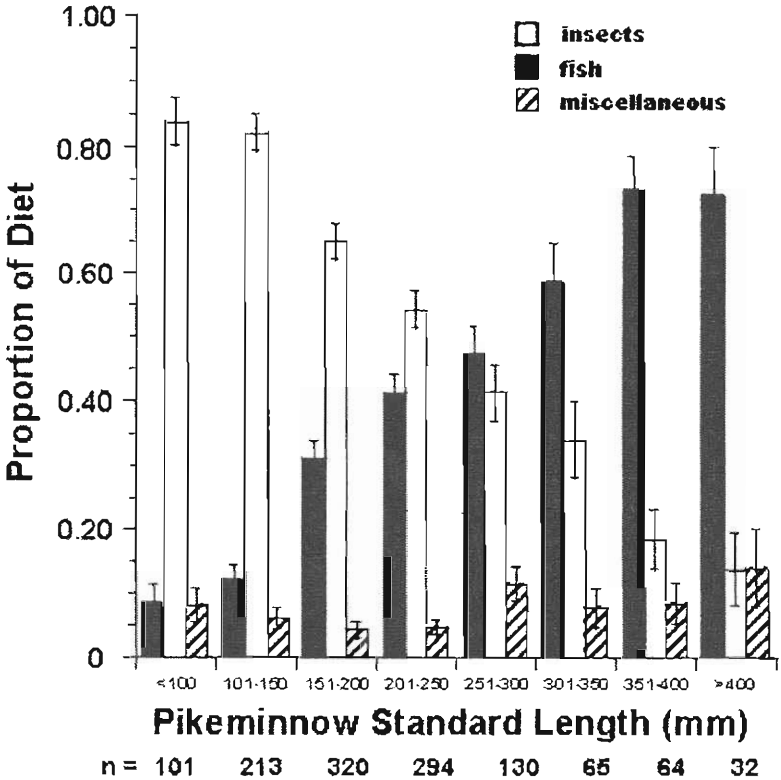


Figure 2. Mean (SE) percent wet weight of fish and insect prey in the diet of Sacramento pikeminnow from the mainstem Eel River and South Fork Eel River, by predator size class. Sample sizes include only fish with food in the foregut.

that Pacific lamprey were less prominent. During the late season, a large portion of the diet of small Sacramento pikeminnow from the MSER consisted of terrestrial insects (31%) while small Sacramento pikeminnow from the SFER focused on Hemiptera, particularly naucoridae (24%). During the early season, sculpins (20%) and lamprey (15%) formed the largest part of the diet of large (> 250 mm SL) Sacramento pikeminnow from the MSER, while large Sacramento pikeminnow from the SFER contained primarily Plecoptera. We did not obtain enough large Sacramento pikeminnow from the MSER to confidently characterize their diet in the late season, but steelhead (23%) and suckers (16%) formed the largest part of the diet of large Sacramento pikeminnow from the SFER.

Individual diet diversities based on the mass of prey varied significantly between rivers ($F_{1,1214}$ = 27.5, p < 0.001) and seasons ($F_{1,1214}$ = 26.1, p < 0.001) (Table 2). Individual diet diversities were significantly higher in the SFER compared to the MSER, and greater during the early season compared to the late season. The river x season interaction ($F_{1,1214}$ = 0.32, $p$ = 0.570) and Sacramento pikeminnow length ($F_{1,1214}$ = 0.86, $p$ = 0.332) were

Table 1. Diet of Sacramento pikeminnow collected from the mainstem Eel River and South Fork Eel River between April 1995 and March 1997. Mean percent by wet weight and (frequency of occurrence) of prey items are presented, with Sacramento pikeminnow categorized by river, season, and size class.

| | Mainstem Eel River | | | | South Fork Eel River | | | |
|---|---|---|---|---|---|---|---|---|
| Season | February - May | | June - October | | February - May | | June-October | |
| Size class (mm SL) | ≤250 | >250 | ≤250 | >250 | ≤250 | >250 | ≤250 | >250 |
| Number of pikeminnow | 353 | 112 | 109 | 13 | 346 | 102 | 120 | 64 |
| Cladocera | 0.0(0.9) | | | | | | | |
| Isopoda | | | | | 0.3(0.3) | 0.5(1.0) | | |
| Astacidae | | | 0.2(0.9) | 7.7(7.7) | | 0.2(1.0) | | 1.3(1.6) |
| Unidentified aquatic insects | 6.8(28.7) | 2.7(0.3) | 8.9(9.3) | 7.7(7.7) | 4.3(6.7) | 1.4(2.0) | 4.9(6.7) | 1.9(3.3) |
| Collembola | | | 0.0(0.9) | | | | | |
| Anisoptera | 3.2(15.7) | 2.1(1.4) | 1.1(1.9) | 0.6(7.7) | 6.2(12.5) | 3.4(8.8) | 5.6(8.4) | 0.1(1.6) |
| Aeshnidae | 0.3(0.9) | | | | 0.1(0.6) | | | |
| Cordulegastridae | | | | | 0.2(0.3) | | | |
| Gomphidae | 5.3(24.0) | 5.0(2.3) | 0.9(0.9) | | 2.7(5.2) | 3.9(10.8) | 0.6(0.8) | 0.0(1.6) |
| Libellulidae | 0.0(0.9) | | | | 0.5(0.9) | | | |
| Macromiidae | 1.2(4.6) | 1.3(0.6) | 0.6(0.9) | | 1.7(3.2) | 1.6(4.9) | 3.8(4.2) | 5.6(6.6) |
| Coleoptera (unk. family) | 1.2(9.3) | 1.1(0.9) | 4.1(5.6) | 3.8(7.7) | 0.0(0.6) | 0.0(1.0) | 0.1(0.8) | 0.0(1.6) |
| Curculionidae | 0.1(0.9) | | | | | | | |
| Dytiscidae | | | | | 0.3(0.3) | | | |
| Elmidae | 0.9(8.3) | | 0.8(1.9) | | 0.1(0.6) | | | |
| Gyrinidae | | | | | 0.1(0.3) | | | |
| Psephenidae | 0.2(1.9) | 0.0(0.3) | | | 0.2(2.0) | 0.0(2.0) | 1.1(1.7) | |
| Diptera (unk. family) | 1.8(10.2) | 0.0(0.3) | 4.6(4.7) | | 0.4(1.2) | | | |
| Ceratopogonidae | 0.2(2.8) | | 0.4(1.9) | | | | | |
| Chironomidae | 0.2(3.7) | | 1.9(2.8) | | 0.4(0.6) | | | |
| Culicidae | 0.0(0.9) | | | | | | | |

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|---|---|---|---|---|---|---|---|---|
| Simuliidae | 0.0(0.9) | | | | | | | |
| Tabanidae | 1.0(3.7) | | 1.1(1.9) | | 0.8(1.7) | 1.0(2.9) | 1.0(3.4) | 0.0(1.6) |
| Tipulidae | 0.6(3.7) | 0.4(0.6) | | | 1.8(9.9) | 0.8(7.8) | 2.0(8.4) | 0.8(8.2) |
| Ephemeroptera (unk. family) | 2.7(13.9) | | 8.6(9.3) | | 0.4(2.0) | 0.0(2.0) | 3.8(6.7) | 2.4(6.6) |
| Baetidae | 1.0(4.6) | | 2.2(3.7) | | 0.1(1.7) | 0.0(1.0) | | |
| Ephemerellidae | | 0.9(0.3) | | | | | 0.0(0.8) | |
| Heptageniidae | 0.7(3.7) | | | | 0.0(0.3) | | | |
| Siphlonuridae | | | 0.9(1.9) | | | | | |
| Tricorythidae | | | | | | | 1.7(1.7) | |
| Hemiptera | | | | | 0.3(0.3) | | 0.1(1.7) | |
| Belastomatidae | | 0.9(0.3) | | | | | | |
| Corixidae | 1.6(6.5) | 0.6(0.6) | 1.0(1.9) | | 0.0(0.3) | | | |
| Naucoridae | 11.9(63.9) | 3.6(2.0) | 7.1(9.3) | 7.7(7.7) | 17.2(35.8) | 8.2(26.5) | 23.8(38.7) | 6.6(18.0) |
| Notonectidae | | | | | | | 0.2(0.8) | |
| Lepidoptera (unk family) | 0.3(0.9) | | | | 0.0(0.6) | | | |
| Pyralidae | | 0.0(0.3) | | | | | | |
| Sphingidae | | | | | 0.1(0.3) | | | |
| Megaloptera | 0.0(0.9) | | | | | | | |
| Corydalidae | 0.2(0.9) | | | | | | | |
| Plecoptera (unk. family) | 5.1(30.6) | 2.3(1.2) | 2.2(4.7) | | 7.2(16.9) | 4.5(9.8) | 6.5(13.4) | 0.7(4.9) |
| Perlidae | 1.3(9.3) | 2.1(0.9) | | | 2.9(4.4) | 5.0(13.7) | 1.8(4.2) | |
| Perlodidae | 3.0(14.8) | 0.8(0.9) | 0.9(0.9) | | 12.4(22.1) | 11.9(22.5) | | |
| Pteronarcyidae | 0.7(2.8) | | | | | | | |
| Trichoptera (unk. family) | 2.2(13.9) | 0.6(0.3) | 1.1(1.9) | | 2.0(4.7) | 0.1(2.9) | 1.5(7.6) | 0.2(3.3) |
| Brachycentridae | 0.1(3.7) | | | | | | | |
| Hydropsychidae | 2.3(19.4) | 0.9(0.6) | 0.1(0.9) | | 2.4(11.3) | 0.0(2.0) | 0.1(3.4) | 0.1(3.3) |
| Limnephilidae | | | | | 0.1(0.6) | 0.3(0.1) | | |
| Sericostomatidae | | | | | 0.1(0.3) | | | |
| Zygoptera | | | | | 0.7(1.7) | 1.0(1.0) | | |
| Calopterygidae | | | | | 0.2(0.9) | 0.4(2.0) | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Coenagrionidae | | | | | 0.4(0.9) | 0.2(2.0) | | |
| Unidentified terrest. insects | 6.5(35.2) | 3.2(1.7) | 30.8(36.4) | | 3.5(9.0) | 2.0(5.9) | 10.5(15.1) | |
| Armadillidae | 0.5(2.8) | | | | 0.7(1.7) | 0.4(4.9) | | 0.0(1.6) |
| Gryllacrididae | | 2.6(1.2) | | | 0.5(0.9) | 1.1(2.0) | | |
| Hymenoptera | | | | | | | 0.0(0.8) | |
| Formicidae | 0.5(5.5) | | | | 0.2(0.9) | | 0.0(0.8) | |
| Labiduridae | 0.1(0.9) | | | | | | | |
| Diplopoda | 0.3(2.8) | | | | 0.2(1.2) | 1.3(4.0) | 0.4(1.6) | |
| Unidentified fishes | 1.2(4.6) | 0.9(0.3) | | 7.7(7.7) | | | 0.6(0.8) | 3.3(3.3) |
| *Ameiurus catus* | | | | | 0.1(0.3) | | | |
| *Catostomus occidentalis* | 3.4(11.1) | 3.6(1.7) | 1.1(1.9) | 7.7(7.7) | 3.8(4.1) | 7.7(10.8) | 4.2(4.2) | 16.0(16.4) |
| *Lepomis cyanellus* | | | | | 0.2(0.3) | | | |
| Cottidae (unk. species) | 1.1(4.6) | 12.5(4.3) | 2.8(2.8) | | 0.9(0.9) | 1.0(1.0) | | |
| *Cottus aleuticus* | | 1.9(0.6) | | | | | | |
| *Cottus asper* | 0.3(0.9) | 5.3(1.7) | 0.9(0.9) | | | | | 1.6(1.6) |
| Cyprinidae (unk. species) | 0.5(1.9) | | | | | | | 1.6(1.6) |
| *Ptychocheilus grandis* | 1.2(4.6) | 2.8(0.9) | 0.9(0.9) | 15.4(15.4) | 4.2(4.7) | 8.3(9.8) | 1.7(1.7) | 8.2(8.2) |
| *Hesperoleucus symmetricus* | 4.8(16.7) | 0.3(0.6) | 0.9(0.9) | 7.7(7.7) | 7.9(9.6) | 4.2(8.8) | 2.5(2.5) | 7.9(9.8) |
| *Gasterosteus aculeatus* | 0.3(0.9) | 3.3(1.7) | 1.9(1.9) | | | 1.5(4.9) | | 1.6(1.6) |
| *Ictalurus nebulosus* | | | | | | | | 1.6(1.6) |
| *Lampetra tridentata* | 13.7(50.0) | 14.9(6.0) | 5.2(5.6) | 7.7(7.7) | 2.6(4.1) | 8.9(14.7) | 1.7(1.7) | 3.2(3.3) |
| *Oncorhynchus* spp. | 2.0(8.3) | 3.6(1.2) | | | 1.4(2.3) | 4.0(6.9) | | |
| *O. mykiss* | 0.3(0.9) | 2.8(0.9) | | 7.7(7.7) | 0.5(0.9) | 6.4(6.9) | 7.5(7.6) | 23.4(26.2) |
| *O. tshawytscha* | | | | | 0.5(0.6) | | | |
| *Diacamptdon tenebrosus* | | 0.8(0.3) | | 7.1(7.7) | | | | |
| *Microtus* sp. | | 0.9(0.3) | | | | | | |
| Ranidae (unk. species) | | 2.0(0.9) | | | 0.4(0.6) | 1.0(1.0) | | |
| *Rana boylii* | | 0.6(0.3) | | | | | | |
| *Sceloporous occidentalis* | | 0.9(0.3) | | | 0 3(0.3) | 0.5(1.0) | | |
| Miscellaneous | 6.8(26.9) | 11.8(4.9) | 6.5(9.3) | 11.5(15.4) | 2.6(4.1) | 5.8(7.8) | 5.4(9.2) | 8.6(9.8) |

Table 2. Mean (SE) Shannon-Wiener individual diet diversity by size class for Sacramento pikeminnow collected from the mainstem Eel River and South Fork Eel River.

| Size class | November - March n | November - March Diversity | April - October n | April - October Diversity |
|---|---|---|---|---|
| Mainstem Eel River | | | | |
| ≤100 | 33 | 0.37(0.08) | 30 | 0.22(0.08) |
| 101-150 | 91 | 0.23(0.04) | 60 | 0.10(0.03) |
| 151-200 | 133 | 0.23(0.03) | 12 | 0.00(0.00) |
| 201-250 | 96 | 0.16(0.03) | 7 | 0.07(0.07) |
| 251-300 | 48 | 0.18(0.04) | 4 | 0.00(0.00) |
| 301-350 | 24 | 0.16(0.06) | 4 | 0.00(0.00) |
| 351-400 | 35 | 0.23(0.07) | 5 | 0.16(0.07) |
| >400 | 5 | 0.27(0.13) | 0 | - |
| South Fork Eel River | | | | |
| ≤100 | 28 | 0.20(0.08) | 10 | 0.18(0.12) |
| 101-150 | 45 | 0.23(0.05) | 17 | 0.36(0.07) |
| 151-200 | 125 | 0.36(0.04) | 50 | 0.26(0.05) |
| 201-250 | 148 | 0.42(0.03) | 43 | 0.25(0.06) |
| 251-300 | 46 | 0.44(0.07) | 32 | 0.18(0.06) |
| 301-350 | 24 | 0.30(0.08) | 13 | 0.16(0.12) |
| 351-400 | 17 | 0.34(0.11) | 7 | 0.08(0.08) |
| >400 | 15 | 0.40(0.12) | 12 | 0.01(0.01) |

not significant terms in the analysis of covariance for Sacramento pikeminnow diet diversity.

The proportion of fish in the diet exhibited different temporal trends in the two rivers (ANCOVA, river x season interaction: $F_{1,1214} = 4.00, p = 0.046$). Sacramento pikeminnow length was a useful covariate in the analysis ($F_{1,1214} = 202.30, p < 0.001$). While the proportion of fish in the diet was similar between rivers during the early season, during the late season the proportion of fish in the Sacramento pikeminnow diet decreased sharply in the MSER while the proportion of fish in the diet of Sacramento pikeminnow from the SFER increased.

The standard length of prey increased with the standard length of Sacramento pikeminnow predators (Fig. 3; $n = 300, r^2 = 0.45, p < 0.001$). Piscivorous Sacramento pikeminnow averaged 266 mm SL (range 84 - 543 mm) while prey fishes averaged 63 mm SL (range 22 - 163 mm SL, excluding one adult lamprey 600 mm total length). The ratio of prey to predator length ranged 0.08 - 0.52.

In contrast to the availability of prey (Table 3), prey selection by large Sacramento pikeminnow did not differ detectably between rivers and seasons. Overall, large Sacramento pikeminnow consumed prey in proportion to estimated prey availability, with the exception of the avoidance of cannibalism (Table 4).

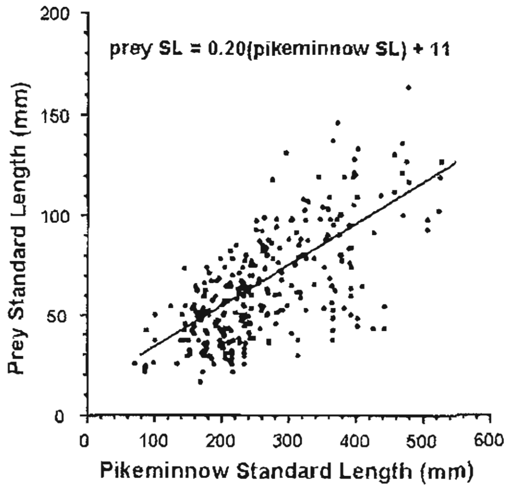


Figure 3. Relationship between the lengths of Sacramento pikeminnow predators and their prey.

Table 3. Mean electrofishing catch-per-unit-effort (SE) from the mainstem Eel River and the South Fork Eel River for pikeminnow prey fishes (< 165 mm SL). We did not sample during November, December, and January to minimize the risk of injury to adult salmonids.

| | Mainstem Eel River | | South Fork Eel River | |
|---|---|---|---|---|
| Season | February-May | June-October | February-May | June-October |
| # sample trips | 50 | 11 | 51 | 13 |
| *Catostomus occidentalis* | 2.9(0.7) | 5.2(2.2) | 1.5(0.5) | 8.1(3.3) |
| *Cottus* spp. | 1.0(0.4) | 1.8(0.8) | 0.4(0.3) | 1.0(0.5) |
| *Gasterosteus aculeatus* | 2.4(1.4) | 5.5(3.9) | 0.1(0.1) | 0.4(0.3) |
| *Hesperoleucus symmetricus* | 7.9(2.4) | 9.6(5.7) | 38.1(17.9) | 36.7(11.0) |
| *Lampetra tridentata* | 89.7(31.9) | 22.1(9.8) | 46.1(11.1) | 17.9(8.7) |
| *Oncorhynchus* spp. | 9.3(2.0) | 3.1(1.8) | 25.4(4.0) | 9.9(5.0) |
| *Ptychocheilus grandis* | 54.3(9.5) | 1,384.8(1288.2) | 73.1(15.8) | 95.2(32.2) |

Both patterns of electivity and overall patterns in food habits indicated that salmonids were not a critical component of the Sacramento pikeminnow diet on the scale of the entire study area. We observed juvenile salmonids in 64 of the 1,219 Sacramento pikeminnow that contained prey in the foregut. These 64 fish had consumed an average of 1.1 salmonids (range 1 - 3). Salmonids made up a small proportion of the diet of Sacramento pikeminnow except for Sacramento pikeminnow > 250 mm SL from the SFER in the late season. In August 1995, at the most upstream SFER site, we collected 29 large Sacramento pikeminnow with prey in the foregut, and 19 of these contained salmonids. Observations by divers revealed high densities of juvenile salmonids in riffles at this site. Overall, body size strongly influenced the tendency to consume salmonids (Fig.

Table 4. Mean (SE) electivities for seven of the most commonly observed vertebrate prey of Sacramento pikeminnow (>250 mm SL) collected from the Eel River, California. Asterisks identify electivities significantly different from zero ($P < 0.0125$).

| | Mainstem Eel River | | South Fork Eel River | |
|---|---|---|---|---|
| Season | February-May | June-October | February-May | June-October |
| # collecting trips | 50 | 11 | 51 | 13 |
| *Catostomus occidentalis* | -0.02(0.02) | -0.05(0.03) | 0.08(0.03) | -0.06(0.03) |
| *Cottus* spp. | 0.12(0.04) | -0.01(0.00) | 0.02(0.02) | 0.06(0.08) |
| *Gasterosteus aculeatus* | 0.01(0.02) | -0.03(0.02) | 0.01(0.01) | 0.07(0.08) |
| *Hesperoleucus symmetricus* | -0.05(0.02) | 0.04(0.10) | -0.07(0.03) | -0.01(0.13) |
| *Lampetra tridentata* | -0.12(0.06) | -0.09(0.06) | -0.08(0.06) | 0.03(0.06) |
| *Oncorhynchus* spp. | -0.05(0.05) | -0.04(0.03) | -0.17(0.06) | -0.02(0.12) |
| *Ptychocheilus grandis* | -0 40(0.04)* | -0.49(0.11)* | -0.29(0.05)* | -0.37(0.10)* |

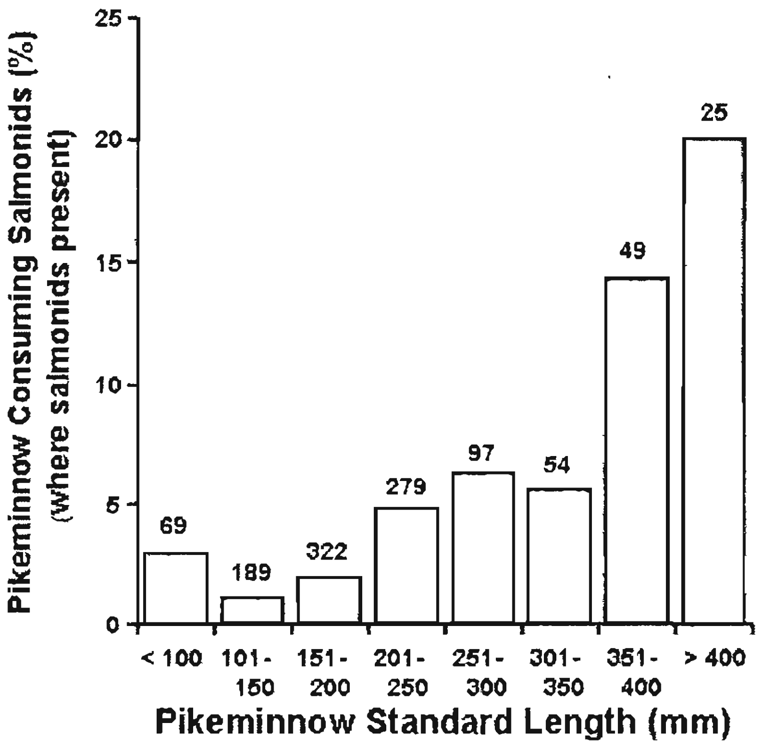


Figure 4. The percent of Sacramento pikeminnow (by size class) that had consumed salmonids at sites where salmonids were present. Numbers above bars indicate sample sizes, which include fish with empty foreguts.

4). Finally, the abundance of Sacramento pikeminnow > 250 mm SL was similar at sites with and without salmonids (catch per unit effort for large Sacramento pikeminnow where salmonids absent: mean = 42.9, SE = 10.7, n = 79; where salmonids present: mean = 38.6, SE = 6.5, n = 27; $t = 0.34$, $p = 0.73$).

## DISCUSSION

The overall patterns in the food habits of Sacramento pikeminnow in this study parallel previous observations from the Eel River and elsewhere. For example, both Brown and Moyle (1997) and Brown (1990) also documented an increase in the consumption of fish with predator body size, although fish were slightly more prevalent in the diets of Sacramento pikeminnow < 250 mm SL in those studies. Although piscivory increases with predator size, Sacramento pikeminnow < 100 mm SL do consume fish (Brown 1990, Merz and Vanicek 1996, Brown and Moyle 1997, this study). Several observations from this and previous studies indicate that the Sacramento pikeminnow is a typical generalist predator with a highly varied diet (Brown 1990, Brown and Moyle 1997). This study adds the observation that the species does not exhibit strong prey selection (with the apparent exception of avoidance of cannibalism). Studies of the northern pikeminnow (*Ptychocheilus oregonensis*) suggest that species also commonly consumes prey in proportion to their availability (Tabor et al. 1993, Petersen et al. 1994, Zimmerman 1999).

Non-selective feeding by Sacramento pikeminnow probably explains the differences in diet diversity we observed across rivers and seasons. Higher diet diversity in the early season probably reflects the availability of more prey types, perhaps in part because of flooded riparian zones and higher activity levels by several prey (e.g., amphibians, lamprey, sculpin). Similarly, differences in prey availability may explain higher diet diversity in the SFER compared to the MSER.

Even if Sacramento pikeminnow do not feed selectively, they may have strong effects on the abundances of some prey. For example, White and Harvey (2001) attributed much lower densities and higher predation risk for sculpin in the Eel River compared to two nearby rivers, to the presence of Sacramento pikeminnow. Brown and Moyle (1997) suggested that predation by Sacramento pikeminnow will also profoundly affect the distribution and abundance of threespine stickleback in the Eel River. Ranid frogs may also be significantly affected by Sacramento pikeminnow, considering the susceptibility of tadpoles and adults during egg deposition.

The only apparent example of selective feeding by Sacramento pikeminnow in this study was the avoidance of cannibalism, even though small Sacramento pikeminnow were abundant in both rivers year round. This behavior was more evident during the late season with the appearance of young-of-the-year pikeminnow. Small Sacramento pikeminnow were routinely observed in association with other prey species, suggesting that differences in habitat use among potential prey does not explain the lack of cannibalism by large pikeminnow. Cannibalism seems unlikely to strongly influence recruitment dynamics or population size of Sacramento pikeminnow, in contrast to some other piscivorous freshwater fishes (Dong and DeAngelis 1998).

Several factors probably contributed to the relatively modest consumption of salmonids by Sacramento pikeminnow we observed. First, because large hatchery releases and impoundments do not occur in the area we studied, it probably contains few particularly high-risk areas for salmonids. High rates of consumption of salmonids by northern pikeminnow in the Columbia River have been closely tied to activities or sites where the prey are aggregated, disorientated, or injured (Buchanan et al. 1981, Vigg et al. 1991, Collis et al. 1995, Ward et al. 1995, Shively et al. 1996). Second, alternative prey were usually abundant compared to salmonids (Table 3). This may partially explain our observation of similar densities of large Sacramento pikeminnow in the presence and absence of salmonids. Third, no competitors for alternative fish prey were present to influence selection for salmonids by Sacramento pikeminnow. Poe et al. (1991) suggested that in the Columbia River other piscivores outcompete northern pikeminnow for non-salmonid prey, thus indirectly increasing northern pikeminnow predation on salmonids. Fourth, relatively high turbidity in the Eel River may favor the consumption of benthic prey (e.g. Pacific lamprey, sculpins, Sacramento sucker). High turbidity can reduce predation risk for juvenile salmonids (Gregory and Levings 1998). Our overall results support the conclusion that pikeminnow are often not significant predators of salmonids under natural conditions in streams (Brown and Moyle 1981).

In contrast to the overall results, most large Sacramento pikeminnow we collected in August at one site in the SFER had consumed salmonids, specifically steelhead. To our knowledge, this site represented the most upstream location of a large school of adult Sacramento pikeminnow in the SFER. Parallel to previous observations of the response of steelhead to large Sacramento pikeminnow (Brown and Moyle 1991, Brown and Brasher 1995), daytime snorkeling observations revealed steelhead concentrated in riffles and large Sacramento pikeminnow in pools at this site. However, radio-tagged Sacramento pikeminnow were found to move into riffles at night at this site (Harvey and Nakamoto 1999). Clearly, stream reaches with thermal regimes and physical habitat that allow occupation by both large Sacramento pikeminnow and steelhead in summer are likely hotspots for predation by the former. The abundance of steelhead relative to other potential prey is usually high in these areas.

The relatively low numbers of salmonids present during our study and the absence of a reliable estimate of predator population size preclude conclusions about the ability of Sacramento pikeminnow to influence salmonid abundance. However, the diverse diet and lack of prey selection we observed suggest that the per predator consumption of salmonids by Sacramento pikeminnow would increase approximately linearly with the abundance of the former. The relationship between body size and salmonid consumption for Sacramento pikeminnow in this study (Fig. 4) and for northern pikeminnow in the Columbia River (Petersen 2001) suggests that, should additional information justify such efforts, predator control should focus on large individuals. After simulation modeling by Rieman and Beamesderfer (1990) identified its potential benefits, this approach reduced predation rates by northern pikeminnow on salmonids in the Columbia River (Friesen and Ward 1999).

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