

Habitat Relationships and Larval Drift of Native and Nonindigenous Fishes in Neighboring Tributaries of a Coastal California River

BRET C. HARVEY,* JASON L. WHITE, AND RODNEY J. NAKAMOTO

U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, California 95521, USA

Abstract.—Motivated by a particular interest in the distribution of the nonindigenous, piscivorous Sacramento pikeminnow *Ptychocheilus grandis*, we examined fish–habitat relationships in small tributaries (draining 20–200 km²) in the Eel River drainage of northwestern California. We sampled juvenile and adult fish in 15 tributaries in both the summer and fall of 1995 and attempted to relate the densities of the most abundant species to physical variables. To determine which species used small tributaries for spawning, we also collected drifting larval fish during the spring of 1996 and 1997. Water temperature, as measured by maximum weekly average temperature, dominated the relationships between physical variables and the densities of age-0 Sacramento pikeminnow, age-0 steelhead *Oncorhynchus mykiss*, California roach *Hesperoleucus symmetricus* (also known as *Lavinia symmetricus*), and Sacramento sucker *Catostomus occidentalis*. Of these groups, only age-0 steelhead were most abundant in cool tributaries. In contrast to results for these groups, temperature regime, instream cover, summer discharge, and water depth contributed approximately equally to the best-fitting models of post-age-0 steelhead abundance. Drift samples revealed widespread use of tributaries for reproduction by both native species and the nonindigenous California roach. We also found drifting larval Sacramento pikeminnows in five streams that ranged widely in size. Temperature regimes in many Eel River tributaries have been affected by both human activities and large floods over the last 50 years. This study suggests that (1) these changes in temperature regime enhanced invasion of the drainage by nonindigenous fishes and (2) management efforts that alter temperature regimes in Eel River tributaries will have significant consequences for the composition of fish assemblages in general and for the effects of Sacramento pikeminnow in particular.

Basic ecological knowledge of nonindigenous species provides the foundation for accurate predictions about their effects on native taxa. Management efforts to influence those effects partially depend on both the ability to predict future distributions of nonindigenous species and knowledge of the habitats necessary to maintain their populations. Alien taxa that are neither game species nor commercially important often present special challenges to resource managers because these taxa rarely have been well-studied.

Since its introduction into the Eel River of northwestern California in about 1980, the Sacramento pikeminnow *Ptychocheilus grandis*, a large cyprinid, has become the most abundant fish in many parts of the drainage. This concerns resource managers because it is known to prey on, and may compete with, regionally depressed salmonids populations (Brown and Moyle 1981). Populations of two salmonid species—*Oncorhynchus mykiss* (both steelhead and rainbow trout) and

coho salmon *O. kisutch*—in the Eel River are listed as threatened under the U.S. Endangered Species Act. Brown and Moyle (1997) pointed out that with the arrival of Sacramento pikeminnow and the earlier introduction of California roach *Lavinia symmetricus*, fish assemblages in the Eel River are now very similar to native assemblages of the neighboring Sacramento–San Joaquin drainage. In that system, coexistence of native cyprinids and salmonids appears to be enhanced by partial longitudinal separation of the two taxa in rivers, cyprinids being concentrated in valley floor and foothill reaches and salmonids in cooler upstream waters (Moyle and Nichols 1973). Brown and Moyle's (1997) extensive sampling of the Eel Drainage after the introduction of Sacramento pikeminnow revealed a similar pattern: Sacramento pikeminnow were most abundant in relatively large channels with low gradients and warm water temperatures, whereas rainbow trout were found predominately in smaller channels with higher gradients and cooler water temperatures. Later studies found Sacramento pikeminnow to be the predominant species in the largest stream channels in the Eel Drainage (B. C. Harvey, unpublished data).

* Corresponding author: bch3@humboldt.edu

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However, Sacramento pikeminnow can also occupy smaller streams with warm water temperatures, and the thermal niches (*sensu* Magnuson et al. 1979) of Sacramento pikeminnow and salmonids such as steelhead and rainbow trout overlap (e.g., Baltz et al. 1987). These points are relevant to the distribution and ecological effects of Sacramento pikeminnow in the Eel Drainage because the drainage includes tributaries that range widely in temperature and historically, tributaries with moderate temperatures may have been particularly productive of steelhead (note, we use steelhead instead of rainbow trout because all of our sampling sites were readily accessible to anadromous fish). Thus, in this study we sought to quantify both the extent to which Sacramento pikeminnow and salmonids co-occur in tributaries of the Eel River and the extent to which their abundances are related to physical variables. The sampling necessary to address these issues allowed us to achieve the broader objective of quantifying relationships of fish and habitat for all the abundant fishes in these tributaries.

While the presence of juvenile and adult Sacramento pikeminnow in a particular tributary may affect competition and predation risk faced by salmonids and other native fishes, the use of tributaries by Sacramento pikeminnow for reproduction has additional ramifications for management of this species. For example, management efforts focused on reducing abundance or reproductive activity of Sacramento pikeminnow in small sections of the drainage are unlikely to be useful if the species is highly mobile and uses a large number of spawning sites. Spawning by Sacramento pikeminnow rarely has been observed in the Eel River drainage, or elsewhere, and the use of Eel River tributaries for spawning by nonsalmonid fishes in general has not been investigated. Thus, we also investigated whether Eel River tributaries provide spawning habitat for Sacramento pikeminnow. The sampling necessary to address this question allowed a general overview of reproduction in tributaries by all the nonsalmonid fishes in the drainage.

Study Sites

The Eel River drainage of northwestern California (Figure 1) encompasses about 9,540 km² of mostly coniferous forest and oak *Quercus* spp. woodlands. The Mediterranean climate produces extreme seasonal differences in discharge. For example, a 7-year discharge record on the East Branch of the South Fork Eel River yielded an

average discharge of 20.0 m³/s in winter and 0.2 m³/s in summer. Vegetation and summer air temperatures vary dramatically within the drainage. Inland portions of the drainage, including the upper mainstem Eel, Middle Fork Eel, North Fork Eel, and upper Van Duzen rivers, are characterized by oak woodlands and hot summers. In contrast, portions of the South Fork Eel, lower mainstem Eel, and lower Van Duzen rivers remain relatively cool in summer because of marine influence (coastal fog). Both redwood *Sequoia sempervirens* forests with varied histories of logging and oak woodlands are common in these lower reaches. The combination of steep gradients in the marine influences on air temperature and vegetation and varied histories of logging yield very different thermal regimes in closely neighboring tributaries of the main channels.

For this study, we selected 15 tributaries that spanned the range of existing thermal regimes and were readily accessible to Sacramento pikeminnow. All tributaries included in this study were within 5 river kilometers of one or more sites in their receiving rivers with high densities of Sacramento pikeminnow. The tributaries were 25–175 km from the mouth of the Eel River; their confluences with larger channels ranged 15–245 m in elevation. Their drainage areas averaged 76 km² (range = 17 – 211 km²). Except for one tributary predominated by old-growth redwood forest, the catchments of all tributaries consisted mostly of second-growth forests or grasslands.

Native taxa in the study streams and in adjacent sections of receiving channels included Pacific lamprey *Lampetra tridentata*, steelhead, chinook salmon *O. tshawytscha*, coho salmon, Sacramento sucker *Catostomus occidentalis*, threespine stickleback *Gasterosteus aculeatus*, coastrange sculpin *Cottus aleuticus*, and prickly sculpin *Cottus asper*. California roach and Sacramento pikeminnow were the most common nonindigenous fish species in the study area, but additional alien species, found almost exclusively in the larger channels, included American shad *Alosa sapidissima*, brown bullhead *Ameiurus nebulosus*, white catfish *Ameiurus catus*, green sunfish *Lepomis cyanellus*, and bluegill *L. macrochirus*. Brown and Moyle (1997) provide a complete description of the fish fauna of the Eel Drainage.

Methods

Juveniles and adults.—To characterize the juvenile–adult fish assemblages of the 15 study tributaries, we sampled fish in single reaches of

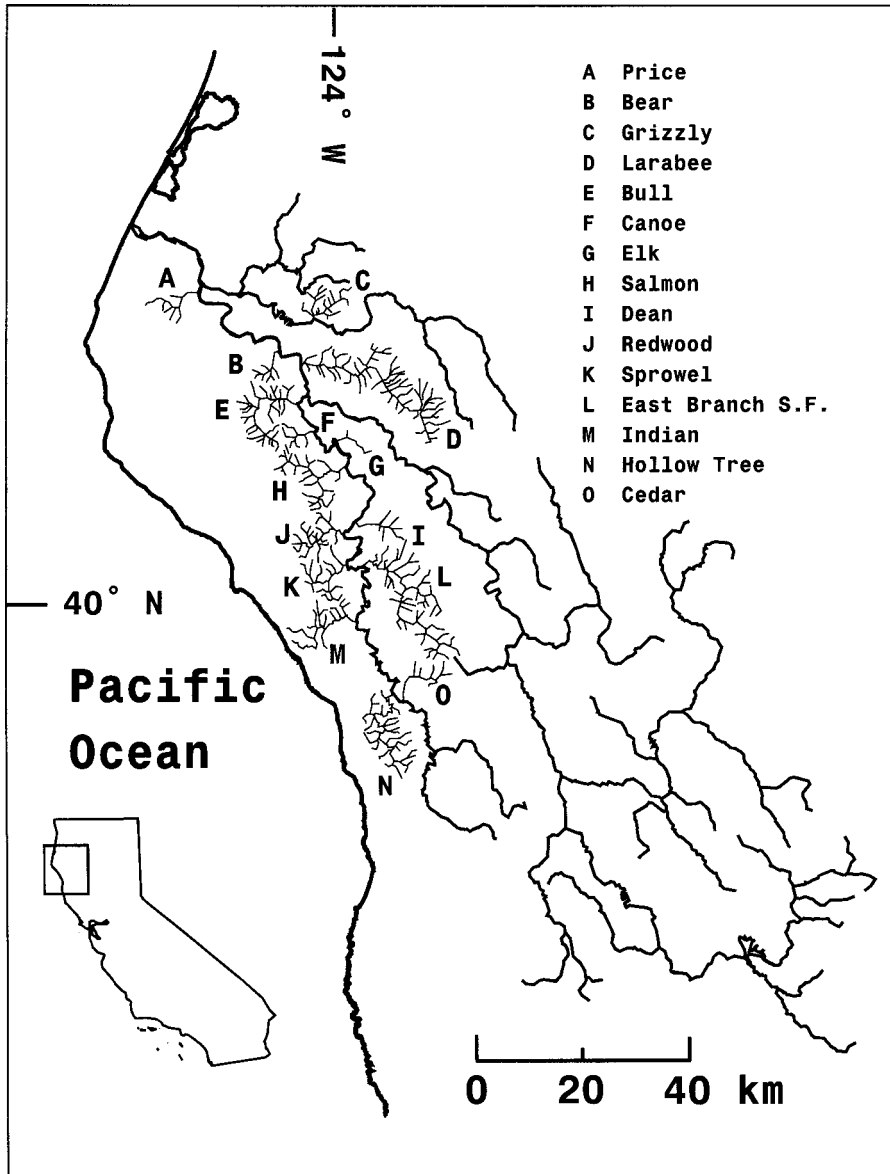


FIGURE 1.—Map of the Eel River drainage of California, showing the drainage networks of tributaries sampled.

each tributary during both summer (6 July–14 August) and fall (2 October–27 October) of 1995. Study reaches averaged 175 m long (range = 60–780 m) and included at least two pools and two riffles. We positioned study reaches near tributary mouths. Gradients of the study reaches averaged 2% (range = 0.5–4.5%). We used multiple-pass electrofishing in 26 of the 30 censuses. All fish captured were identified and counted, and at least 50 individuals of each year-class of each species were measured. Large pools prevented effective

electrofishing in two streams. For the four censuses in those streams, we used visual observations while snorkeling to count fish and estimate their lengths to the nearest 10 mm.

After sampling juvenile and adult fishes, we measured several physical habitat characteristics within sampling reaches. In each mesohabitat (e.g., pools, riffles), we estimated substrate composition (as percent of the substrate in each of six categories: silt, sand, gravel, cobble, boulder, bedrock) and measured the maximum depth, wetted

width at a minimum of three evenly spaced transects, and depth at three evenly spaced points along each transect. We also measured the area of structures throughout each reach that provided in-stream cover for fish 100 mm or more total length (TL). Finally, we measured stream discharge with a top-set wading rod and electronic current meter.

We recorded water temperature in the study reaches in both 1995 and 1996 using dataloggers set in shaded, well-mixed sites. Dataloggers recorded water temperature every 1.2 h. Data collection was limited to August–September in 1995. To more completely examine thermal regimes and to be certain we measured the highest annual temperatures, we measured water temperatures from May through October in 1996. In 1996 we summarized the temperature data for each stream by computing maximum weekly average temperature (MWAT), which has been used to describe relationships between thermal regime and the distribution of fish (e.g., Eaton et al. 1995). We considered 1996 temperature data useful in the analysis of fish data from 1995 because (1) average water temperatures in the tributaries in 1995 and 1996, over the dates for which we had overlapping data, were highly correlated ($r = 0.95$, $N = 10$ streams); (2) no differences within streams between years exceeded two times the reported accuracy of the dataloggers (maximum difference within a stream between years = 1.2°C); and (3) we observed no physical changes between years that might have altered the temperature regime of any stream relative to the other streams in the data set.

We separately analyzed the abundances of all taxa that represented at least 5% of the total catch. In our analyses we further separated age-0 and post-age-0 Sacramento pikeminnow and steelhead because of their importance to resource managers and because we anticipated size-specific differences in habitat use by these species. To analyze fish densities with linear models at the stream scale, we used the averages of summer and fall fish densities as response variables. (Inspection of separate analyses of summer and fall data revealed similar results to those obtained by averaging the two sampling periods.) Discharge, water depth, MWAT, and the availability of cover were selected a priori as independent variables for this analysis. Water depth was the average depth of all the habitat units sampled, weighted by the area of those units. The availability of cover was the total area of cover in each reach sampled divided by the total area of the reach. We used the average of summer

and fall discharge, water depth, and cover values as input to the models. Because we had no a priori basis for exclusion of any specific models that included the four independent variables, we compared models representing all possible subsets of these variables. To reduce the risk of overfitting statistical models to a relatively small number of observations, we included in the analyses only the four available independent variables we considered most likely to influence the abundance of Sacramento pikeminnow and steelhead. The same consideration prevented us from including transformations of, and interactions among, physical variables in our analyses.

We evaluated models using Akaike's information criterion adjusted for small samples (AIC_c) and estimates of the posterior relative probabilities for each model (Burnham and Anderson 1998); AIC_c reflects an information-theory-based approach to estimating the fit between candidate models and data. This approach allows comparison of models with varying numbers of parameters, incorporating the fact that the variability of estimates of model parameters increases with the number of independent variables. Posterior relative probabilities indicate the probability that each model is the best-fitting model, given the data, and the assumption that one of the candidate models represents the "best" model. The estimates were derived from AIC_c and the assumption of equal prior probabilities for all models (Burnham and Anderson 1998). We estimated the probability that the best-fitting model for each response variable contained a particular independent variable by summing the probabilities of all candidate models that included that independent variable.

Larval drift.—We collected drift samples for larval fishes in 14 of 15 tributaries where we sampled juveniles and adults. In general, we took drift samples in each stream once between 11 June and 2 July 1996 and two to five times between 13 May and 24 June 1997. We placed drift nets in tributaries within 30 m of their confluences with a larger channel (main stems of the Eel, South Fork Eel, or Van Duzen rivers). Because of locally high gradients and water velocities at tributary mouths, combined with the limited swimming ability of larval fish, we considered the capture of larvae of a given species strong evidence of spawning in the tributary by that species. At each site, we also collected drift in the receiving channel just upstream from its confluence with the tributary. We timed sampling to maximize the probability of encountering larval Sacramento pikeminnow, using

published life history information (Moyle 1976), existing data on seasonal patterns of water temperature in the Eel River and its tributaries, and our observations of the reproductive condition of Sacramento pikeminnow in the lower main stems of the Eel and South Fork Eel rivers.

Sampling effort in both tributaries and receiving channels consisted of deploying two nets (45-cm \times 30-cm opening, 360- μ m mesh) for 20–60 min beginning 30 min to 4 h after sunset. The length of deployment was adjusted so that individual nets filtered 100 m³ or more of water. We sampled at night because preliminary data and other studies (Harvey 1991; Kennedy and Vinyard 1997; Marchetti and Moyle 2000) indicated that larval stream fishes drift more at night in relatively clear streams. We positioned nets to capture surface water, but nets usually spanned the entire water column because water depths were less than 30 cm. To the extent allowed by depth and water velocity, we positioned one net near the stream margin and the other near midchannel. We measured water velocity through the nets with an electronic current meter. Samples were preserved in 5% formalin.

In the laboratory, we used a dissecting microscope with an ocular micrometer to identify, enumerate, and measure larval fishes. We examined whole samples, except for 5 of 196 samples that were subsampled using a plankton splitter. Fish larvae were identified to species, except for prickly sculpin and coastrange sculpin, which we could not differentiate. Lamprey ammocoetes also were not identifiable to species. A small fraction of the ammocoetes we captured may have been river lamprey *Lampetra ayresi* rather than Pacific lamprey, although the former has been reported only once from the Eel River.

Using logistic regression, we attempted to relate the presence or absence of larval pikeminnow among tributaries to watershed area and average water temperature during the spawning period (May–June). Unfortunately, complete temperature records were limited, allowing us to include only 11 streams in this analysis.

Results

Juveniles and Adults

Physical habitat differed substantially among tributaries. The MWAT ranged from 17.7°C to 24.5°C. The averages of summer and fall discharge measurements varied from 0.01 to 0.27 m³/s among tributaries. Discharge declined between sampling periods from a mean for the 15 tributaries

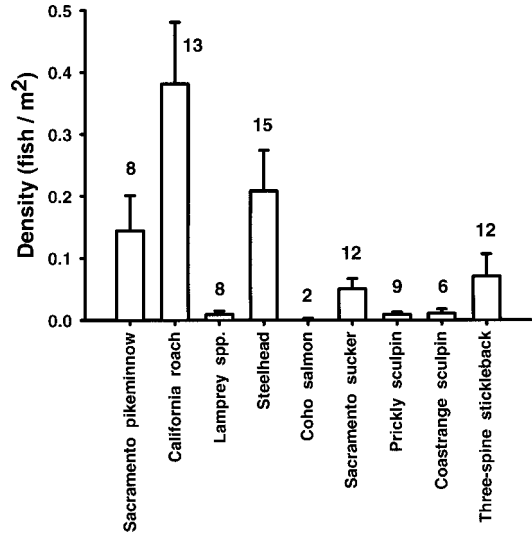


FIGURE 2.—Overall densities (+1 SE) of juveniles and adults of the nine fish species captured in 15 tributaries of the Eel River drainage of California. Numbers above bars indicate the number of tributaries in which a species was observed.

of 0.17 m³/s in the summer to 0.04 m³/s in the fall. Mean discharge was not strongly predicted by drainage area ($r^2 = 0.22$), probably because of significant variation among watersheds in vegetation and the extent of sediment storage in channels. Mean depth in the study reaches, combining summer and fall data, ranged from 9 to 45 cm and averaged 28 cm. Instream cover was not common; we estimated that an average of 4.5% (range = 1–19%) of the wetted area of tributaries provided cover. Fine substrate predominated on stream bottoms; among tributaries, a mean of 53% (range = 24–92%) of the stream bottom consisted of gravel or finer substrate. The four variables used in the analyses of fish abundance at the stream scale (MWAT, discharge, depth, cover) were not significantly correlated with one another.

We found nine species of fish in the study streams, and enumerated more than 27,000 juvenile and adult fish. California roach was the most abundant species overall (Figure 2); steelhead was the only species found in all tributaries. We captured or observed mostly small fish: 94% were less than 100 mm TL. Size-frequency distributions indicated that young-of-year fish accounted for large proportions of the total number of individuals for species that commonly exceed 100 mm TL by age-1 (steelhead = 79%; Sacramento pikeminnow = 85%; Sacramento sucker = 93%). We collected post-age-0 steelhead in all 15 streams, but only

TABLE 2.—Summary of analyses by 15 models that were conducted separately by species and used to predict the abundance of fishes in tributaries of the Eel River. The cumulative relative probabilities of the 8 models including each of the four independent variables are provided (e.g., the probabilities of the following models are summed for temperature: temperature, temperature + depth, temperature + cover, temperature + discharge, temperature + depth + cover, temperature + depth + discharge, temperature + cover + discharge, temperature + depth + cover + discharge). For Sacramento pikeminnow, results in parentheses reflect an analysis conducted after removal of one outlying observation.

Variable	Age-0 Sacramento pikeminnow	Age-0 steelhead	Post-age-0 steelhead	California roach	Sacramento sucker
Temperature	0.99 (>0.99)	0.99	0.49	0.90	0.92
Depth	0.52 (0.22)	0.51	0.46	0.50	0.19
Cover	0.22 (0.15)	0.19	0.56	0.19	0.23
Discharge	0.17 (0.27)	0.17	0.51	0.58	0.27

el compared with the other independent variables (Table 2).

In contrast to models for age-0 Sacramento pikeminnow and age-0 steelhead, independent variables other than temperature were important in the analysis of post-age-0 steelhead abundance. In fact, the two best models of post-age-0 steelhead abundance included different pairs of independent variables (cover and discharge versus temperature and depth; Table 1). All four independent variables had similar posterior probabilities of inclusion in the actual best-fitting model for post-age-0 steelhead (Table 2).

We separately analyzed three additional species that each represented more than 5% of the total catch. Temperature as summarized by MWAT was a relatively strong predictor of the abundance of California roach and Sacramento sucker (Table 3), and both species were more abundant in warmer tributaries. For California roach, the best-fitting model, as determined by AIC_c , included a negative relationship with stream discharge and a positive relationship with water depth (Table 2). For Sacramento sucker, the simple relationship with MWAT provided the best-fitting linear model (Table 2). None of the four habitat variables, separately or in combination, strongly predicted the density of threespine stickleback ($r^2 = 0.19$ for the best-fitting model).

Larval Drift

We captured larval fish or lamprey ammocoetes at all sites in the larger channels and in all tributaries sampled except Elk Creek, a small, cool stream that we sampled only once (Table 3). More than 33,000 individuals were collected overall. Larval native fishes (Sacramento sucker, threespine stickleback, and the two sculpin species) and lamprey ammocoetes were widely distributed among tributaries and larger channels. The three

alien species captured exhibited several spatial patterns of drift. We found American shad only in the lower section of the main stem of Eel River. California roach larvae were common in tributaries throughout the study area. Larval Sacramento pikeminnow drifted at particularly high rates in Salmon Creek and at lower levels only in tributaries of the South Fork Eel River, within 40 river kilometers upstream of Salmon Creek. Except for lamprey and American shad, we found the highest concentrations of each species in tributaries rather than at sites in receiving channels.

The presence or absence of larval Sacramento pikeminnow in tributaries was not predicted well by logistic regression with drainage area and average May–June temperature as independent variables. Although Sacramento pikeminnow reproduced in the largest, warmest tributaries, we also found larval Sacramento pikeminnow in Dean Creek, one of the smaller streams in the data set, and in Sprowel Creek, which had one of the coolest average temperatures for May–June.

Overall Patterns by Life History Stage

To examine overall patterns of tributary use, we categorized the presence–absence of species by life history stage (Table 4). We separated adults and juveniles by size using published species-specific information (Lee et al. 1980). Although within-year and among-year variation in presence–absence of species and life stages in tributaries weaken the reliability of results for specific streams, we think this approach can identify broad patterns. Both California roach and threespine stickleback are capable of completing their life cycles within single tributaries. We also found all life stages of sculpin in all the tributaries where one or both of the two sculpin species were common. However, the presence of juveniles probably reflects immigration from larger channels, given

TABLE 3.—Mean densities (fish/1,000 m³) of drifting larval fishes in the Eel River drainage of California, May–July 1996–1997. Asterisks identify nonindigenous species.

Location	Longitudinal position (km) ^a	Drainage area (km ²)	Number of sample dates	Species						
				Sacramento pikeminnow*	California roach*	American shad*	Sculpin spp.	Threespine stickleback	Sacramento sucker	Lamprey spp. (ammocoetes)
Tributary sites										
Price Creek	25	34	3	0	321	0	0	20	0	0
Bear Creek	53	22	3	0	0	0	<1	<1	0	0
Grizzly Creek	58	50	5	0	4	0	<1	<1	0	8
Larabee Creek	59	211	2	0	95	0	<1	34	131	3
Bull Creek	68	108	3	0	0	0	10	<1	9	29
Canoe Creek	76	27	3	0	0	0	513	0	0	7
Elk Creek	86	17	1	0	0	0	0	0	0	0
Salmon Creek	92	94	5	218	124	0	34	<1	149	31
Dean Creek	109	37	3	2	911	0	0	0	0	0
Redwood Creek	113	67	3	<1	30	0	3	2	0	4
Sprowel Creek	125	60	3	2	11	0	165	2	<1	20
East Branch South Fork	130	198	4	3	29	0	0	5	80	76
Indian Creek	149	73	3	0	1	0	0	<1	14	2
Hollow Tree Creek	175	107	3	0	2	0	0	1	48	4
Main stem sites										
Eel River	25	8,132	3	0	<1	2	0	11	<1	0
	53	7,931	3	0	0	<1	0	<1	4	9
	59	7,676	2	0	0	<1	0	5	<1	16
Van Duzen River	58	575	5	<1	5	0	5	5	24	9
South Fork Eel River	68	1,674	3	0	<1	0	0	0	2	7
	76	1,620	3	0	<1	0	0	<1	<1	<1
	86	1,573	1	0	0	0	4	0	0	325
	92	1,461	4	<1	<1	0	5	0	<1	1
	109	1,333	3	2	3	0	<1	0	3	11
	113	1,246	3	<1	0	0	0	0	<1	3
	125	1,145	3	0	0	0	<1	0	3	5
	130	935	3	0	<1	0	<1	<1	5	135
	149	805	3	0	0	0	0	0	1	<1
	175	528	3	0	<1	0	0	<1	4	2

^a Longitudinal position indicates distance upstream from the ocean.

TABLE 4.—Presence–absence of life stages of fishes in tributaries of the Eel River of California. Adults and juveniles of a species were classified as present if they were collected in either of two sampling periods, July–August 1995 or October 1995. Presence (1) or absence (0) is indicated sequentially for larvae, juveniles, and adults (e.g., 1/1/0 indicates the presence of larvae and juveniles and the absence of adults). One of the study streams (Cedar Creek) is not included because no collections of larvae were made there.

Tributary	Species				
	Sacramento pikeminnow	California roach	Sculpin spp.	Threespine stickleback	Sacramento sucker
Price	0/0/0	1/1/1	0/0/1	1/1/1	0/0/0
Bear	0/0/0	0/0/0	1/0/1	1/1/1	0/1/0
Grizzly	0/0/0	1/1/1	1/0/1	1/0/1	0/0/0
Larabee	0/1/1	1/1/1	1/1/1	1/1/1	1/1/0
Bull	0/1/0	0/1/1	1/1/1	1/1/1	1/1/0
Canoe	0/0/0	0/0/0	1/1/1	0/0/0	0/1/0
Elk	0/0/0	0/0/1	0/0/0	1/1/0	0/0/0
Salmon	1/1/0	1/1/1	1/0/1	1/1/1	1/1/0
Dean	1/1/0	1/1/1	0/0/0	0/0/0	0/1/0
Redwood	1/1/0	1/1/1	0/0/1	1/1/1	0/1/0
Sprowel	1/1/0	1/1/1	1/0/0	1/1/1	1/1/1
East Branch South Fork	1/1/1	1/1/1	0/0/0	1/1/1	1/1/0
Indian	0/1/0	1/1/1	0/0/1	1/0/1	1/1/0
Hollow Tree	0/0/0	1/1/1	0/0/0	1/1/1	1/1/0

the propensity of larvae of these two species to drift and their use of main-stem and estuary habitat. (Brown et al. 1995 provides a complete description of the life histories of the two sculpin species in the Eel River.)

Although most of the tributaries we sampled did not contain adults of the largest nonanadromous fishes (Sacramento pikeminnow and Sacramento sucker), many tributaries provide habitat for reproduction and juvenile rearing by these species. Immigration into tributaries from receiving channels by juveniles of these species is apparently common; we found juvenile Sacramento pikeminnow and Sacramento suckers in several tributaries in which we did not capture any larvae. Juveniles may enter tributaries most frequently in late summer. For example, in the three creeks where juvenile Sacramento suckers were the only life stage of that species collected, they were captured only in the fall.

Discussion

Variation in water temperature is frequently correlated with longitudinal zonation in lotic fish assemblages (Rahel and Hubert 1991; Paller 1994) and with variation in the distribution and biomass of stream fishes at the regional or larger scale (Fausch et al. 1994; Sowa and Rabeni 1995; Stoneman and Jones 2000). This study shows that variation in water temperature also may explain differences in the abundance of fishes in similar-sized, closely neighboring tributaries of a single drainage. Temperature remains an important abiotic factor across spatial scales and may often deserve primary consideration during efforts to conserve fishes and restore habitat (e.g., Rabeni and Sowa 1996).

Temperature may influence the abundance of fishes by both direct and indirect mechanisms. For example, the opposing responses of juvenile Sacramento pikeminnow and steelhead to variation in water temperature in this study are not entirely explained by the species' physiological tolerances. The metabolic rate of Sacramento pikeminnow is relatively constant over 15–25°C compared with other California stream fishes (Cech et al. 1990). Juvenile steelhead, on the other hand, are physiologically limited by water temperatures of 24–25°C or more (Myrick 1998), but they can achieve relatively high densities in some streams where MWATs are around 20–22°C, such as Hollow Tree Creek. Perhaps not coincidentally, Hollow Tree Creek also lacked Sacramento pikeminnow. Temperature-dependent interactions between Sacra-

mento pikeminnow and steelhead may influence their abundances in Eel River tributaries. In laboratory experiments, growth of territorially dominant juvenile steelhead was insensitive to the addition of juvenile Sacramento pikeminnow when water temperatures ranged 15–18°C, but Sacramento pikeminnow depressed growth of dominant steelhead by as much as an equal number and biomass of steelhead when temperature ranged from 20°C to 23°C (C. D. Reese and B. C. Harvey, unpublished data). Temperature-dependent interactions among stream fishes may commonly influence their distribution and abundance (Baltz et al. 1982; Cunjak and Green 1986; Reeves et al. 1987; De Staso and Rahel 1994).

Although temperature regime was clearly important to the distribution and abundance of juvenile steelhead, the two age groups we studied responded differently to variation in physical habitat. Although MWAT was the dominant explanatory variable in the analysis of age-0 steelhead, all physical variables included in our analyses apparently influenced the abundance of post-age-0 steelhead. Abundance of older, larger juvenile steelhead may tend to be greater in deeper habitats for several reasons. Larger individuals may experience greater risk of predation by terrestrial predators in shallow water (Harvey and Stewart 1991). Also, the intraspecific competitive effect of age-0 steelhead on larger juveniles may increase in shallower water (Harvey and Nakamoto 1997). The positive influence of instream cover on post-age-0 steelhead also may be related to predation risk. In addition, instream cover may increase overwinter retention of juvenile steelhead in tributaries. In the small streams we studied, higher summer discharge may positively influence the abundance of post-age-0 steelhead by increasing the quantity of microhabitat that provides efficient foraging opportunities for large juvenile salmonids; streams with very low discharge offered few areas combining at least moderate depth or cover and substantial water velocities. Finally, the relation of age-0 steelhead abundance to water temperature may have been more strongly negative than for the abundance of older steelhead because the effects of competition and predation by juvenile Sacramento pikeminnow may be more severe for smaller steelhead, and pikeminnow were more abundant in warmer streams.

The species-temperature relationships we observed for juveniles and adults of four species paralleled results from a larger-scale analysis of Eel River fish assemblages by Brown and Moyle

(1997). However, that study encompassed a broad range of stream sizes over which water temperature, depth, and stream discharge were positively correlated, so it distinguished relationships between fishes and physical variables that were not apparent in our study. For example, over the entire range of stream sizes in the drainage, positive relationships between the abundance of Sacramento pikeminnow and both stream discharge and depth equaled or exceeded any patterns related to summer water temperature. Similarly, there were strong negative relationships between these same variables and the abundance of steelhead. In our study, which included only tributaries draining about 20–200 km², the abundance of Sacramento pikeminnow appeared unrelated to discharge and possibly negatively related to water depth. The abundance of steelhead appeared, if anything, positively related to water depth and discharge, which is also contrary to the results of the larger-scale study. Clearly, conclusions of research on fish–habitat relationships are influenced by the range of physical conditions examined. Differences in the results of the two Eel River studies are enhanced by the fact that the different ranges of stream sizes examined also influenced the size ranges of individuals observed, particularly for Sacramento pikeminnow.

In contrast to patterns in the abundances of older fish, the presence–absence of both alien and native larval fishes in tributaries appeared less strongly related to water temperature, possibly because of the relatively narrow range of water temperatures available among tributaries during the peak period of reproduction. Average temperature in May–June ranged only from 13.3°C to 17°C among tributaries; thus, all the study streams probably provide adequate thermal regimes for spawning by Sacramento pikeminnow and other resident fishes. Our results leave open the possibility that thermal regime was related to the total reproductive effort in tributaries by one or more species, but the intensity of sampling did not allow us to estimate that more sensitive response variable. For some species, features of adjacent receiving channels may be more important than small differences in water temperature in determining the distribution of spawning among tributaries. For example, all five tributaries where we captured larval Sacramento pikeminnows are near large, deep pools in the South Fork Eel River, which provide habitat for adults. Although some adult Sacramento pikeminnows make apparent upstream spawning movements, exceeding 90 km in the Eel River

(Harvey and Nakamoto 1999), at some locations adults in the larger channels may spawn locally, perhaps in nearby tributaries. Tributaries near the upstream end of our study area in the South Fork Eel River may be less likely to be used for spawning by Sacramento pikeminnows because adults are less common in the river compared with downstream reaches and because riffles upstream in the main channels may be more suitable for spawning than those downstream.

Reproductive activity by lamprey and nonanadromous native fishes was widespread among the tributaries we sampled, and tributary habitat may be important to the persistence of several species in the Eel River drainage. Although all life history stages of the species collected in tributaries also occupy larger channels, the latter have become riskier habitats for small fishes since the introduction of Sacramento pikeminnow. For example, predation risk for sculpin is about 20 times higher in the large channels of the Eel River compared with nearby rivers lacking Sacramento pikeminnows (White and Harvey 2001). Even if predation risk from avian and terrestrial predators is relatively high in tributaries because they are shallower than larger streams, tributaries probably offer habitats with lower overall predation risk compared with larger channels, particularly for small fishes. Although threespine stickleback may be particularly susceptible to predation by Sacramento pikeminnow (L. R. Brown, U.S. Geological Survey, unpublished data), this species may persist in the drainage in part because of its ability, perhaps unique among the native fishes, to complete its life cycle in small streams.

The importance of thermal regime to the success of Sacramento pikeminnow in tributaries of the Eel River is significant from both historical and management perspectives. Following extensive anthropogenic disturbance of the landscape, large floods in the 1950s and in 1964 caused dramatic changes to many watersheds in the Eel River drainage. Widespread landslides and loss of riparian vegetation caused long-term changes that continue to influence summer stream temperatures. This study suggests that those changes enhanced the extent of invasion of the drainage by Sacramento pikeminnow (and California roach) decades later. Contemporary management plans and activities that promote restoration of riparian vegetation in tributary watersheds may reduce the range and ecological effects of Sacramento pikeminnow in the drainage while also enhancing habitat for native salmonids. Considering current conditions in

the drainage, management approaches should take into account mechanisms linking the extent of riparian vegetation to channel stability and peak flows, that are in turn affected by sediment supply and the condition of hillslopes. Sediment supply rates and the dynamics of riparian vegetation affect not only the thermal regimes of tributaries, but also other features of instream habitat (surface discharge, water depth, cover) that this study suggests are important to juvenile steelhead.

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