

Invading species in the Eel River, California: successes, failures, and relationships with resident species

Larry R. Brown¹ & Peter B. Moyle

Department of Wildlife, Fisheries and Conservation Biology, University of California, Davis, CA 95616, U.S.A.

¹*Present address: U.S. Geological Survey, 2800 Cottage Way, Rm. W-2234, Sacramento, CA 95825, U.S.A.*

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Synopsis

We examined invasions of non-native fishes into the Eel River, California. At least 16 species of fish have been introduced into the drainage which originally supported 12–14 fish species. Our study was prompted by the unauthorized introduction in 1979 of Sacramento squawfish, *Ptychocheilus grandis*, a large predatory cyprinid. From 1986 to 1990, we conducted growth and diet studies of squawfish, conducted intensive surveys of the distribution and habitat associations of both native and introduced species, and examined the nature of species-habitat and interspecies relationships. We found no evidence for increased growth or expanded feeding habits, compared to native populations, of Sacramento squawfish as they invaded the Eel River drainage. Ten of the introduced species were well established, with four species limited to a reservoir and six species established in streams. The success or failure of introductions of stream species appeared to be a function of the ability of a species to survive the fluctuating, highly seasonal, flow regime. The present mixture of native and exotic species has not formed stable fish assemblages but it seems likely that four habitat-associated assemblages will develop. The overall effect of the successful species introductions has been to assemble a group of species, with some exceptions, that are native to and occur together in many California streams. The assemblages now forming are similar to those found in other California streams. The assemblage characterized by squawfish and suckers is likely to be resistant to invasion, in the absence of human caused habitat modifications.

Introduction

The native biotas of freshwater and estuarine systems are in rapid decline throughout the world (Moyle & Leidy 1991, Allan & Flecker 1993), at least partially because of introductions of exotic species (Moyle 1986). However, not every species invasion results in extinction of native species. Communities recovering from Pleistocene climate change and glaciation, including much of North

America (Ricklefs 1987), seem especially likely to incorporate new species (Lodge 1993a). Consequently, attempts to predict the outcome of introductions into aquatic systems generally have failed (Li & Moyle 1981, Lodge 1993b, Moyle & Light 1996a) and introductions often have resulted in undesirable outcomes (Moyle et al. 1986). Studies of the effects of introduced species on resident species and how exotic species become incorporated into communities are needed, so dynamics of invaded

Table 1. Ecological characteristics of native and introduced fishes of the Eel River drainage, exclusive of estuarine species. For introduced species, source and date of introduction are given. Species introduced into Pillsbury Reservoir are indicated by an asterisk.

Species	Source ¹	Present status ²	General habitat use ³	Eel River habitat use ⁴	Trophic category ⁵	Temperature category ⁶
Native species						
Pacific lamprey, <i>Lampetra tridentata</i>	N	–	AN	AN	DT,PR	CD
Pacific brook lamprey, <i>Lampetra richardsoni</i>	N	?	LT	LT	DT	CD
Green sturgeon, <i>Acipenser medirostris</i>	N	0	AN	AN	PR	CD–WM
Longfin smelt, <i>Spirinchus thaleichthys</i>	N	0 ⁷	AN	AN	ZOO	CD–WM
Coho salmon, <i>Oncorhynchus kisutch</i>	N	–	AN	AN	INV,PR	CD
Chinook salmon, <i>Oncorhynchus tshawytscha</i>	N	–	AN	AN	INV,PR	CD
Pink salmon, <i>Oncorhynchus gorbuscha</i>	N	0	AN	AN	INV,PR	CD
Chum salmon, <i>Oncorhynchus keta</i>	N	0	AN	AN	INV,PR	CD
Rainbow trout, <i>Oncorhynchus mykiss</i>	N	–	AN,LN,LT	AN,SR	INV,PR	CD
Cutthroat trout, <i>Oncorhynchus clarki</i>	N	–	AN	AN	INV,PR	CD
Sacramento sucker, <i>Catostomus occidentalis</i>	N	=	LT	SR	OMN	CD–WM
Prickly sculpin, <i>Cottus asper</i>	N	=	AM,LT	AM,SR	INV	CD–WM
Coastrange sculpin, <i>Cottus aleuticus</i>	N	=	AM,LT	AM,SR	INV	CD
Threespine stickleback, <i>Gasterosteus aculeatus</i>	N	–	AN,LT	AN,SR	INV	CD–WM
Introduced species						
American shad, <i>Alosa sapidissima</i>	EUS, 1872–1939	–	AN	AN	ZOO	WM
Threadfin shad, <i>Dorosoma petenense</i> *	EUS, ca. 1980	=	LN	RR	ZOO	WM
Golden shiner, <i>Notemigonus chrysoleucas</i> *	EUS, pre–1961	=	LN	RR	ZOO	WM
Fathead minnow, <i>Pimephales promelas</i>	EUS, ?	?	LT	SR	OMN	WM
California roach, <i>Lavinia symmetricus</i> *	CA, ca. 1970	=	LT	SR	OMN	WM
Sacramento squawfish, <i>Ptychocheilus grandis</i> *	CA, ca. 1979	+	LT	SR	INV,PR	WM
Speckled dace, <i>Rhinichthys osculus</i>	CA, pre–1986	=	LT	SR	INV	CD–WM
Brown bullhead, <i>Ameiurus nebulosus</i> *	EUS, pre–1939	=	LN,LT	SR,RR	INV	WM
Green sunfish, <i>Lepomis cyanellus</i> *	EUS, pre–1939	=	LT	SR	INV,PR	WM
Bluegill, <i>Lepomis macrochirus</i> *	EUS, pre–1939 ⁸	=	LN	RR	INV	WM
Largemouth bass, <i>Micropterus salmoides</i> *	EUS, 1986	+	LN	RR	INV,PR	WM
Brook charr, <i>Salvelinus fontinalis</i> *	EUS, 1960s	0	LN,LT	NA	INV,PR	CD
Brown trout, <i>Salmo trutta</i> *	EUS, 1960s	0	LN,LT	NA	INV,PR	CD
Kokanee, <i>Oncorhynchus nerka kennlyi</i> *	BC, 1960s	0	LN	NA	ZOO	CD
Ayu, <i>Plecoglossus altivelis</i>	JAP, 1960s	0	AM	NA	INV,PR	CD
White catfish, <i>Ameiurus catus</i>	EUS, 1990s ⁹	?	LN,LT	?	INV	WM

¹ Source: EUS = eastern United States, CA = California, JAP = Japan, BC = British Columbia.

² Status: 0 = extinct or rare; – = declining; = = populations relatively stable; + = increasing; ? = trend unknown.

³ General habitat use in California or native region: AN = anadromous, AM = amphidromous, LT = lotic, LN = lentic.

⁴ Habitat use in the Eel River drainage: AN = anadromous, AM = amphidromous, SR = stream resident, RR = reservoir resident.

⁵ Trophic status: INV = invertivore, ZOO = zooplantivore, OMN = omnivore, PR = predator on fish, large invertebrates, or other large prey. When two designations, appear the first refers to juveniles and the second to adults.

⁶ Temperature category: CD = cold water, WM = warm water

⁷ S. Cannata, California State University at Humboldt, personal communication.

⁸ Shapovalov (1939) reported bluegill as possibly being present based on unverified reports. Because all subsequent species lists include bluegill we assume the unverified reports were correct.

⁹ R. Nakamoto personal communication.

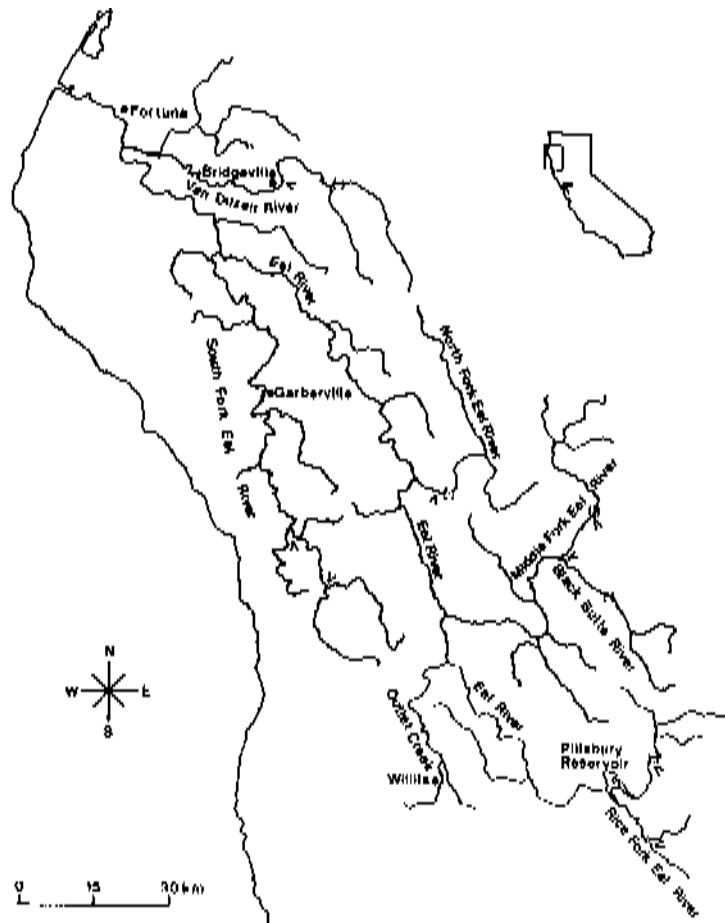


Figure 1. The Eel River drainage and the locations of barriers (h) that limit the ranges of some species and may limit the upstream dispersal of Sacramento squawfish. The upstream limit of squawfish distribution by the end of this study is shown (>). The upstream limit of squawfish in the South Fork Eel River as of summer 1992 (M. Power personal communication) is also shown.

communities can be better understood and the accuracy of predictions improved.

We examined invasions of non-native fishes into the Eel River, a large coastal river system in northern California. The study was prompted by the unauthorized introduction of Sacramento squawfish, *Ptychocheilus grandis*, a large predatory cyprinid, into the river about 1979. We began studies of the ongoing invasion of the drainage by squawfish in 1986 and documented effects on the resident fishes (Brown & Moyle 1991). At least 15 other species of fish have been introduced into the drainage (Table 1). We were able to document the success of each concurrent with studying the squawfish invasion.

The original fish fauna of the Eel River consisted of six anadromous species, two species with both

anadromous and resident populations, two species with both resident and amphidromous populations, and two resident species (Table 1). Two additional anadromous species were likely present. The low number of resident species was unusual for such a large coastal California drainage (Moyle 1976). In part because of its importance for the production of anadromous salmon and trout, the Eel River drainage largely has been protected from water diversions, except for one reservoir (Pillsbury Reservoir) and an associated diversion dam (Cape Horn Dam) in the upper reaches of the mainstem Eel River (Figure 1). However, the drainage was not protected from erosion related to timber harvest and road-building. Major floods in 1955 and 1964 resulted in losses of riparian vegetation and in deposition of

sand and gravel into the streambed (Lisle 1982). This has resulted in a major reduction in the anadromous fish populations from which the system has still not recovered. The anadromous fish populations suffered additional stress when a major drought (1987–1992) reduced stream flows, access to spawning areas, and rearing habitat for juvenile fishes.

Ten fish species have been introduced into Pillsbury Reservoir (Table 1). Seven have established reproducing populations in the reservoir, which now serves as a source of introduced fishes for the entire drainage. This situation is at least partially responsible for the ongoing shift of the Eel River drainage from a system dominated by native anadromous fishes to one dominated by introduced resident fishes, although not all introduced species are equally successful. Ecologically, the most significant of the invaders are the California roach, which affects the algae and benthic invertebrate communities (Power 1990) and Sacramento squawfish, which causes shifts in spatial distribution of the resident fishes (Brown & Moyle 1991, Brown & Brasher 1995).

In this study, we address several issues concerning the characteristics of introduced species and the relationships of introduced species, especially squawfish, with the native fish fauna of the Eel River. First, we studied the ecology of invading squawfish, as characterized by growth and diet, to determine if Eel River populations were different from native populations in other California streams. Second, we examined published and unpublished records to determine the history of fish introductions to the Eel River drainage. We used our survey data and other data sources to determine the present status and distribution of native and introduced species and to suggest possible reasons for the increase or decline of each species. Third, we examined species co-occurrence to determine if groups of native and exotic species formed recognizable assemblages. Analyses of species-habitat relationships were used to assess the role of physical habitat in forming any such groups.

Study area

The Eel River system is the third-largest drainage in

California, collecting water from the Coast Ranges in Mendocino, Lake, Humboldt, and Trinity counties. The mainstem of the Eel River is about 350 km long, from headwaters (maximum elevation ca. 600 m) to the Pacific Ocean and includes four major tributaries, from south to north: Middle Fork (MF) Eel River, North Fork (NF) Eel River, South Fork (SF) Eel River, and the Van Duzen River (Figure 1). Precipitation is seasonal, with most during the winter and spring. There is little or no snowpack; precipitation runs off quickly, resulting in high flows following storms. Low flows occur from May through October (Palmer et al.¹).

The watershed is a mixture of public and private forest and rangelands. Pine forests dominate the vegetation of the headwater areas of the upper mainstem Eel River, MF Eel River, NF Eel River, and Van Duzen River drainages. Oak woodlands dominate the remainder of the NF and MF Eel River drainages and the middle portion of the Van Duzen and mainstem Eel River drainages. Much of the lower mainstem Eel River, and Van Duzen Rivers are surrounded by coastal redwood, *Sequoia sempervirens*, forests. The SF Eel River is almost entirely within the coastal redwood belt except the extreme headwaters that are in oak woodlands.

Although some of the redwoods are protected in state parks and other reserves, most of the drainage has been heavily logged, and most of the old growth has been harvested since World War II. Heavy machinery developed during the war permitted logging of previously inaccessible, steep, highly erodible slopes (S. Downie personal communication). The resulting exposure of these soils combined with record rainfalls in 1955 and 1964 caused massive flooding and erosion in the drainage, followed by the deposition of 10–20 m of gravel and sediment in the main channels (Lisle 1982). After these floods, the stream channels became wide and shallow, with few deep pools and little riparian vegetation

¹ Palmer, JR., M.F. Friebe, L.F. Trujillo & K.L. Markham. 1993. Water resources data California water year 1993, vol. 2, Pacific slope basins from Arroyo Grande to Oregon state line, except Central Valley. U.S. Geological Survey Water-Data Report CA-93-2. 391 pp.

(Jones²). The channels have shown some recovery from the events, as sediment is gradually washed downstream, but much of the watershed is still eroding at accelerated rates. Anadromous fish populations declined precipitously following the 1964 flood and have not recovered (California Department of Fish and Game (CDFG) unpublished data, Lufkin 1991).

The only major water project in the drainage, Pillsbury Reservoir, was built in 1921. Water is released from the reservoir into the river channel for a distance of 19 km and is then diverted at Cape Horn Dam to the Russian River drainage to the south. The diversion provides both hydroelectric power and water for various uses. The result is a section of river between Pillsbury Reservoir and Cape Horn Dam with artificially enhanced flows of cool water during the summer months. The rest of the drainage was protected from development by placing it in California's Wild and Scenic River system in 1972 and in the national Wild and Scenic River system in 1982.

Methods

Growth and diet of Sacramento squawfish

We used scale analysis to determine the size of squawfish at the end of each year of growth. Scales from Sacramento squawfish were removed from below the tip of the left pectoral fin, cleaned and mounted between glass slides. Scales were viewed using a scale reader (23X magnification). Distances from focus to edge and from focus to annuli were measured to the nearest millimeter. Backcalculated lengths at each age were calculated using Fraser's (1916) proportionality formula:

$$\ln L_a = a + (\ln S_a \div \ln S_r) \times (\ln L_c - a),$$

where: L_a = length of the fish at annulus formation, S_a = distance from focus to annulus, S_r = distance from focus to edge, L_c = length at capture, and a = the intercept value of a regression of the natural logarithm of fish length on the natural logarithm of scale radius. Ages were validated by comparison to peaks in length-frequency histograms.

We calculated mean backcalculated length and standard deviation for each age group from each area for each year in which a collection was made. We combined data across years and compared mean backcalculated length at age among areas using one-way analysis of variance. We then compared growth rates of Eel River squawfish to published and unpublished data from other areas.

Throughout the study we preserved samples of squawfish in 10% formalin for analysis of feeding habits. In the laboratory, each fish was measured to the nearest mm standard length (SL) and weighed to the nearest 0.01 g. The contents of the gut were then removed and weighed on an electronic balance to the nearest 0.0001 g. Squawfish were separated into 50 mm SL size classes for analyses. Items in the gut were identified to the lowest taxon possible and the percentage of each taxon present estimated. Percentages of each taxon in the diet were estimated by calculating the estimated mass of each taxon in individual stomachs (measured total mass $\times$ estimated proportion), summing over all individuals, and calculating an overall percentage for each size class. Frequencies of occurrence (percentage of stomachs in which a particular taxon occurred) were also calculated.

We compared diet breadth of Eel River squawfish with that of squawfish from Bear Creek, a small stream in the Sacramento River drainage (Brown 1990). Data were grouped at equivalent taxonomic levels for calculations. Niche breadth was calculated as follows (Levins 1968):

$$B_i = 1 / \sum (p_{ij})^2,$$

where p_{ij} is the proportion of item j in the diet of species i . Diet breadth of the two populations were compared with a Mann-Whitney U test. Niche breadth of each 50 mm size class common to both populations were the data used in the test.

² Jones, W.E. 1980. Summer steelhead (*Salmo gairdneri*) in the Middle Fork Eel River and their relationship to environmental changes, 1966 through 1978. California Department of Fish and Game, Anadromous Fisheries Branch Administrative Report No. 80-2. 25 pp.

Status and distribution of native and introduced species

We examined published and unpublished data addressing the date of introduction of exotic species. The present status of native and introduced species, compared to historical population levels, were determined from published articles, unpublished data, and data collected in this study (see below for methods). We documented life history, general habitat requirements, and trophic category of each species. This information was obtained from published and unpublished literature with precedence given to California sources. We related present status to the ecological characteristics of each species. In addition, details of the past and present distribution of

selected common species are given as determined from this study and past records.

Fish assemblages and species-habitat relationships

We sampled fish by electroshocking, seining (estuary only), snorkeling, or both snorkeling and electroshocking depending on physical conditions at each station. Most sampling was conducted from mid-June to mid-September 1987 to 1989. Limited sampling was conducted during April and May of 1989 and 1990. Most sites were only sampled once during the study. A few stations were sampled several times, usually to document upstream movement of squawfish. We sampled a reach of stream

Table 2. Comparison of backcalculated lengths for squawfish from Rice Fork Eel River, Eel River between Pillsbury Reservoir and Cape Horn Dam, Eel River below Cape Horn Dam, and South Fork Eel River. Backcalculated lengths at each age were compared among areas with one-way analysis of variance followed by Bonferroni pairwise comparisons. Means that are not significantly different are indicated by similar superscripts. Backcalculated lengths for squawfish from Pillsbury Reservoir (B. Bridges unpublished data) are shown for comparison.

Variable	Age					
	1	2	3	4	5	6
Rice Fork Eel River						
Mean	60 ^a	143	220	263 ^a	311	381
SD	12	37	35	36	56	71
N	81	63	58	38	10	2
Between Pillsbury Reservoir and Cape Horn Dam¹						
Mean	67 ^a	150	232	303 ^b	353	401
SD	14	40	41	44	43	60
N	95	56	36	23	15	6
Below Cape Horn Dam						
Mean	64 ^a	136	206	300 ^{a, b}	361	327
SD	14	41	55	71	64	30
N	70	51	27	10	5	2
South Fork Eel River						
Mean	77 ^b	138	229	—	—	—
SD	15	20	9	—	—	—
N	249	91	2	—	—	—
ANOVA results	p < 0.001	NS	NS	p < 0.01	NS	NS
Pillsbury Reservoir 1985						
Mean	73	149	227	275	329	383
N	103	55	44	33	14	3
Pillsbury Reservoir 1986						
Mean	102	163	218	274	402	
N	70	67	54	12	2	

¹ One 7 year old fish was also captured. Its backcalculated length at age 7 was 407 mm SL.

that included all locally available habitat types. Most sample reaches were at least 50 m long. All fish captured were counted and measured (SL $\pm$ 1 mm). Visual counts of small fish or those which evaded capture were also recorded. When snorkeling, one or two researchers swam in an upstream direction and counted individuals of all species present and estimated their length (SL $\pm$ 5 mm). An abundance code was assigned to total fish abundance where 1 = rare, 2 = uncommon, 3 = common, 4 = abundant, and 5 = superabundant.

In addition to the fish sampling, we measured water temperature ($^{\circ}$ C), maximum depth (cm), and stream discharge ($\text{m}^3 \text{sec}^{-1}$) and estimated average depth (cm), mean width (m), turbidity (1–5 scale: 1 = crystal clear to 5 = extremely turbid), percent area covered by attached algae, percentages of pool, riffle, and run habitat at the site, percent of the water's surface which was apparently shaded most

of the day, percent of the water's surface providing cover as surface turbulence, and substrate composition as percentages of mud, sand, gravel, rubble, boulders and bedrock. Stream order, gradient (m km^{-1}), and elevation (m) were determined from U.S. Geological Survey 7.5' or 15' topographical maps.

At sites sampled more than once during a year or in several years, species distributions included all species caught in at least one of the samples. For quantitative analyses (below) only data from the most recent sample were used. Species that were observed during sampling for other studies (Brown & Moyle 1991) were listed at the nearest survey station for analyses of distribution. We analyzed species abundances as relative abundances. Species which occurred in more than 10% of the samples were included in the quantitative analyses, except for lampreys which we did not sample efficiently.

Table 3. Diet of Sacramento squawfish by size class (mm, SL) from the Eel River drainage, California. Values are percentage by mass with frequency of occurrence in parentheses.

Prey	Size class									
	1–50	51–100	101–150	151–200	201–250	251–300	301–350	351–400	401–450	451–500
N =	48	72	116	87	9	2	5	1	4	1
Trichoptera	8 (19)	2 (15)	2 (15)	1 (16)	+ (11)	–	+ (20)	–	–	–
Ephemeroptera	57 (65)	8 (22)	16 (25)	23 (24)	+ (11)	–	–	–	–	–
Diptera	6 (13)	5 (29)	1 (6)	+ (3)	+ (22)	–	–	–	3 (25)	–
Plecoptera	2 (2)	11 (14)	3 (5)	2 (9)	14 (11)	–	1 (20)	100 (100)	+ (25)	–
Megaloptera	–	10 (11)	+ (2)	–	–	–	–	–	–	–
Lepidoptera	–	+ (1)	–	–	–	–	–	–	–	–
Hemiptera	10 (17)	9 (10)	14 (35)	8 (38)	+ (11)	–	–	–	–	–
Coleoptera	–	–	1 (2)	–	–	–	–	–	–	–
Odonata	–	–	3 (3)	–	–	–	–	–	–	–
terrestrials	2 (10)	+ (3)	2 (4)	+ (1)	5 (22)	–	–	–	–	–
misc. Insecta	6 (23)	12 (33)	2 (13)	+ (14)	1 (22)	–	–	–	–	–
Gastropoda	–	–	+ (1)	2 (3)	–	–	–	–	–	–
Crustacea	+ (2)	1 (6)	–	–	–	–	–	–	–	–
Decapoda	–	–	–	–	4 (11)	72 (50)	98 (80)	–	2 (50)	100 (100)
Fish										
Sacramento squawfish	–	–	4 (3)	–	12 (11)	–	–	–	65 (25)	–
Sacramento sucker	–	8 (1)	–	+ (1)	–	–	–	–	–	–
California roach	–	27 (6)	17 (5)	13 (5)	–	–	–	–	–	–
Salmonids	–	–	2 (1)	10 (2)	47 (22)	28 (50)	–	–	–	–
Lampreys	–	–	5 (3)	15 (13)	–	–	–	–	–	–
Threespine stickleback	–	–	3 (3)	5 (9)	–	–	–	–	–	–
unidentified	–	–	13 (9)	14 (15)	13 (22)	–	–	–	30 (25)	–
Amphibia	–	6 (3)	9 (16)	2 (12)	3 (11)	–	–	–	–	–
animal debris	11 (13)	1 (13)	2 (10)	4 (9)	+ (11)	–	–	–	–	–

Mud, silt and sand were combined into a single substrate category designated 'fines' for analyses because of many zero values for the first two categories. Bedrock was combined with boulder for the same reason. All data were transformed to improve normality for statistical analyses. Physical variables measured as percentages and fish relative abundances were arcsine transformed. Gradient, elevation, average depth, maximum depth, and average width were $\log_e(x)$ transformed and stream discharge was $\log_e(x+1)$ transformed.

Species relationships were assessed with principal components analysis (PCA) of the transformed relative abundance data from each sampling reach. The resulting principal components (PCs) were examined to determine if sampling reaches could be separated on the basis of species composition. Only PCs with eigenvalues greater than one were interpreted. We conducted a canonical correlation analysis (CCA) between species relative abundances and physical variables at each sampling reach to determine if patterns in species abundance were correlated with physical variables. A high correlation would imply that fish assemblages observed were the result of responses to physical habitat. To aid in

the interpretation of CCA results we analyzed species-specific relationships with physical habitat. We conducted a PCA on the physical variables to obtain a reduced number of composite variables. Only PCs with eigenvalues greater than 1 were retained for further analysis. We then calculated Pearson product-moment correlations between species relative abundances and the physical PCs. Because of the large number of sites sampled, even extremely low correlation coefficients were statistically significant. We arbitrarily considered only correlation coefficients ≥ 0.45 to have ecological significance (coefficients of this magnitude account for 20 percent of the variance). Correlations of total fish abundance (1–5 scale) with physical PCs were calculated to determine the response of abundance of all fish to physical gradients.

Results

Growth and diet of Sacramento squawfish

The oldest squawfish collected was age 7 (Table 2). Sample sizes were inadequate for comparisons

Table 4. Number of sites where a species was observed, during this study, in the subdrainages of the Eel River drainage system.

Species	Mainstem Eel River (N = 161)	Van Duzen River (N = 36)	South Fork Eel River (N = 75)	North Fork Eel River (N = 37)	Middle Fork Eel River (N = 61)	Black Butte River (N = 25)	Rice Fork Eel River (N = 17)	Total (N = 412)
Native species								
Rainbow trout	84	36	71	27	52	25	16	314
Sacramento sucker	89	19	35	7	18	1	5	174
Threespine stickleback	46	14	32	0	0	0	1	93
Prickly sculpin	24	12	11	0	0	0	0	47
Pacific lamprey	10	13	19	0	0	0	0	42
Coastrange sculpin	11	13	8	0	0	0	0	32
Coho salmon	0	3	6	0	0	0	0	9
Chinook salmon	2	0	0	0	1	0	0	3
Pacific brook lamprey	0	0	0	0	0	0	3	3
Introduced species								
California roach	107	18	44	28	24	8	1	230
Sacramento squawfish	100	11	11	3	23	1	7	156
Green sunfish	21	0	4	0	0	0	0	25
American shad	14	0	0	0	0	0	0	14
Brown bullhead	7	0	0	0	0	0	0	7
Speckled dace	0	5	0	0	0	0	0	5
Bluegill	3	0	0	0	0	0	0	3
Largemouth bass	1	0	0	0	0	0	0	1

among years at specific areas, so the data were combined across years. Backcalculated lengths at age for Eel River squawfish fell well within the range of values for Sacramento River drainage populations (Brown 1990), providing no evidence that squawfish were growing faster or larger in the Eel River drainage, including Pillsbury Reservoir (Table 2, B. Bridges unpublished data). The larger size at age 1 in the SF Eel River, the most recently established population, suggested that young-of-year fish in newly established populations may grow faster than in more mature populations (Table 2). However, the difference disappeared by age 2. At age 4, squawfish from the Rice Fork Eel River were smaller than those from the reach between the dams but this difference disappeared at age 5. The lack of consistent differences in length at age among the different areas indicated that conditions for growth were relatively similar throughout the drainage.

Squawfish < 100 mm SL ate mostly Ephemeroptera, Trichoptera, Diptera, and Hemiptera (Table 3). Fishes appeared in the diet of squawfish 51–100 mm SL and were increasingly important in larger size classes. Crayfish were important in the diet of squawfish > 200 mm SL in the river between Pillsbury Reservoir and Cape Horn Dam and frogs and tadpoles were important in the Rice Fork Eel River. Salmonids were an important item for squawfish > 100 mm SL (100% of diet) in the mainstem Eel River at the confluence of Outlet Creek in May 1989.

The feeding habits of squawfish in the Eel River drainage were similar to those of squawfish from the Sacramento River drainage. In Bear Creek (Sacramento River drainage), squawfish began consuming fishes at 51–100 mm SL and fishes made up more than 50% of the diet in squawfish 101–150 mm SL (Brown 1990). In the Eel River drainage, fish also first appeared in the diet at 51–100 mm SL but did not make up more than 50 percent of the diet until 151–200 mm SL (Table 3).

Niche breadths for Eel River squawfish ranged from 1.84 for fish 201–250 mm SL to 5.55 for fish 51–100 mm SL. The range in niche breadth for Bear Creek fish was somewhat wider ranging from 1.86 for fish 201–250 mm SL to 7.15 for fish 51–100 mm SL. Diet breadth tended to decline for larger fish

because adult squawfish specialized on fishes instead of more diverse invertebrate prey. Diet breadth of the Eel River squawfish was not significantly different from that of the Bear Creek population (Mann-Whitney $U=11.0$, $p > 0.05$). Eel River squawfish fed opportunistically on abundant novel prey items. Lamprey ammocoetes, frogs, and tadpoles were common prey but they have not been recorded in diets of Sacramento squawfish from other areas (Taft & Murphy 1950, Moyle 1976, Brown 1990, P. Moyle unpublished data). Juvenile salmonids (mainly chinook salmon) also were consumed opportunistically, primarily during the spring outmigration.

Status and distribution of native and introduced species

Twelve native species have been reported from the drainage (Table 1), ten of them wholly or partially diadromous (anadromous or amphidromous). All the anadromous species or species with anadromous populations have declined. Pink and chum salmon probably inhabited the drainage in the past, based on past overall distributions in California (Moyle et al.³), but there are no definitive records of their presence. Only Sacramento sucker (stream resident) and the two sculpins (stream resident/amphidromous) have populations that seem relatively stable. The decline of rainbow trout is mostly due to declines in the anadromous populations (steelhead rainbow trout). Threespine stickleback have declined based on the loss or decline of several upstream populations. The status of Pacific brook lamprey is unknown because it is difficult to sample and there are no early accounts of its distribution or abundance.

Rainbow trout, including both anadromous and resident populations, was the most widespread of any species (Table 4). In general, trout were abundant in cool headwater and tributary streams. They were absent from the lower mainstem Eel River

³ Moyle, P.B., R.M. Yoshiyama, J.E. Williams & E.D. Wikramanayake. 1995. Fish species of special concern of California. California Department of Fish and Game, Sacramento. 272 pp.

where they have previously been observed (Brown⁴).

Sacramento suckers were present in all the major drainages (Table 4) but were not widespread or abundant. Adult suckers were relatively rare and observed only in deep pools. Young-of-year suckers were rarely observed in large numbers. The largest concentrations of suckers were in the lower 62 km of the SF Eel River, the lower 51 km of the Van Duzen River, and the mainstem Eel River downstream from Pillsbury Reservoir (271 km from the ocean) in areas where large, deep pools were common.

Threespine sticklebacks were most abundant in the lower reaches of the Van Duzen River and mainstem Eel River, throughout the SF Eel River, and in the estuary (Table 4). Sticklebacks were also present in the upper Eel River from the Rice Fork Eel River to the confluence of Outlet Creek, including the Outlet Creek drainage (this study, P. Steiner unpublished data). Sticklebacks have also been reported from the MF Eel River up to 253 km from the ocean (Jones²) and the NF Eel River a distance of 209 km from the ocean (CDFG unpublished data) but we did not observe them in those streams. Sticklebacks have recently been observed in an area of the MF Eel River we did not survey (B. Harvey personal communication). Interpretation of the status of stickleback is complicated by the possibility that upstream populations may have been the result of accidental introductions during inter- and intra-drainage transfers of anadromous fishes that occurred on the north coast of California from 1938 into the 1960s (W. Jones personal communication).

Prickly sculpin were only observed in the mainstem Eel River (to 116 km from the ocean), SF Eel River (to 122 km from the ocean), and Van Duzen River drainages (to 66 km from the ocean) (Table 4). Prickly sculpins were present, but usually not abundant, in many of the cool tributary streams. Coastrange sculpin were almost as abundant as prickly sculpin but did not meet the criteria for quantitative analysis (present at 10% of the 401 sites

with physical data). Distribution of the two sculpin species were very similar but the upstream limit of prickly sculpin appears to be determined by physical conditions and that of coastrange sculpin appears to be determined by upstream dispersal from the estuary (Brown et al. 1995).

Sixteen species have been introduced to the drainage (Table 1). Ten of the species were originally introduced into Pillsbury Reservoir. Twelve species are still present, though the status of fathead minnow and white catfish (first specimens collected subsequent to our study) are unknown because their presence has been established on the basis of just a few collections.

Three of the four unsuccessful species, brook charr, brown trout, and kokanee, are coldwater species introduced into Pillsbury Reservoir (Anderson⁵). The fourth unsuccessful species, the amphidromous Japanese ayu, was introduced into the river several times in the 1960s but never became established (Moyle 1976).

The anadromous introduced species, American shad, invaded the Eel River system sometime between its introduction into the Sacramento-San Joaquin drainage of California in 1892 and 1939 when it was already well established (Shapovalov⁶). American shad runs have declined along with the native anadromous species.

The nine non-migratory introduced species form three groups: (1) four species that are largely confined to Pillsbury Reservoir; (2) two species that are present in the reservoir but have small downstream populations as well; and (3) three California stream species with populations ranging from widespread in the drainage to restricted in extent but possibly expanding. The first group includes threadfin shad, golden shiner, bluegill, and largemouth bass. Threadfin shad and golden shiner have been cap-

⁴ Brown, C. 1980. Standing crops and distribution of fishes in selected reaches of the Eel River system. California Department of Fish and Game, Anadromous Fisheries Branch Administrative Report No. 80. 12 pp.

⁵ Anderson, K.R. 1972. Report to the California State Water Resources Board by the Department of Fish and Game regarding water applications 18785 and 18786, Eel River, Lake and Mendocino counties. California Department of Fish and Game, Environmental Services, Sacramento. 65 pp.

⁶ Shapovalov, L. 1939. Recommendations for management of the fisheries of the Eel River drainage basin, California. California Department of Fish and Game, Bureau of Fish Conservation Administration Report 39-2. 20 pp.

tured in downstream migrant traps located below the reservoir, near Cape Horn Dam (Day⁷, R. Kruger unpublished data, P. Steiner unpublished data) and we observed a few bluegill and one largemouth bass in surveys within 20 km downstream of Pillsbury Reservoir. However, none of these species appear to have established reproducing stocks in downstream areas. Largemouth bass, the most recent introduction, was introduced into Pillsbury Reservoir in 1986 by the California Department of Fish and Game as a Sacramento squawfish control measure.

The second group includes green sunfish and brown bullhead. Both species are established in the reservoir but have small scattered stocks in downstream areas as well. Both were present in the drainage by the 1930s. We observed green sunfish in the mainstem Eel River and the SF Eel River (Table 4) in small, warm pools or along the edges of larger pools, usually associated with aquatic vegetation or large boulders. In the mainstem Eel River, green sunfish have been reported from Pillsbury Reservoir, downstream to the estuary (Shapovalov⁶, Murphy & DeWitt⁸, Fisk & Pelgren⁹, Brown^{4,10}). They have also been reported from the MF Eel River as far as 47 km upstream from the mainstem. We observed brown bullheads at sites between 116 and 232 km from the ocean in the mainstem Eel River and in the lower reaches of Outlet Creek. Earlier studies indicate a distribution similar to that of the green sunfish in the mainstem Eel River (Shapovalov⁶, Murphy & DeWitt⁸, Brown^{4,10}). We are not certain if the few brown bullheads and green sunfish represent permanently established populations in

downstream areas or are the result of periodic colonization from Pillsbury Reservoir. These two species are particularly likely to become established during periods of prolonged drought, such as occurred during the study period.

The three invading California stream species are California roach, Sacramento squawfish, and speckled dace. All three species are native to the nearby Sacramento-San Joaquin River drainage system to the east and to different coastal systems to the south (roach and squawfish) and north (dace) (Moyle 1976). California roach were introduced into the drainage around 1970 and colonized most of the suitable habitat in the drainage in 10–15 years (Fite 1973, Brown^{4,10}), although the invasion was poorly documented. Roach was the most widely distributed introduced species (Table 4). It was also the most abundant species we observed. The correspondence of the upstream limit of roach with physical barriers on the MF Eel River, Black Butte River, and Van Duzen River (Figure 1) suggests that they could potentially be more widespread in the drainage. Roach were present in a number of tributary streams throughout the Eel River drainage but were generally restricted to the lower reaches. In the cool tributaries, the abundance of roach was generally less than that of trout.

Sacramento squawfish were introduced into Pillsbury by unknown individuals in about 1979 or 1980. Young-of-year squawfish were first collected downstream from the reservoir in 1980 (R. Kruger unpublished data). In 1986, the first year of our study, squawfish were present throughout the mainstem Eel River and had colonized the lower 47 km

⁷ Day, J.S. 1968. A study of downstream migration of fish past Cape Horn Dam on the upper Eel River, Mendocino County, as related to the Pacific Gas and Electric Company's Van Arsdale diversion. California Department of Fish and Game, Marine Resources Administrative Report 68–4. 15 pp.

⁸ Murphy, G.I. & J.W. DeWitt, Jr. 1951. Notes on the fishes and fishery of the lower Eel River, Humboldt County, California. California Department of Fish and Game, Bureau of Conservation Administrative Report No. 51–9. 30 pp.

⁹ Fisk, L.O. & O.E. Pelgren. 1955. A limnological survey of Lake Pillsbury, Lake County, California. California Department of Fish and Game, Inland Fishers Administration Report No. 57–30. 12 pp.

¹⁰ Brown, C. 1976. A study of the distribution of fishes in the Eel River, 1975. California Department of Fish and Game, Region 1, Contract Services Section Information Report No. 76–3. 9 pp.

Table 5. Principal component loadings for relative abundances of the six most common species in the Eel River drainage (N = 401). Component loadings of less than 0.3 are indicated by an *.

Species	PC1	PC2
Rainbow trout	– 0.99	*
Prickly sculpin	*	0.74
Threespine stickleback	0.40	0.65
Sacramento squawfish	0.59	*
California roach	0.74	– 0.45
Sacramento sucker	0.43	0.36
Percent of variance explained:	37.1	22.1
Cumulative variance explained:	37.1	59.2

of the MF Eel River, the lower 56 km of the SF Eel River, and the lower 37 km of the Van Duzen River. By the end of our study, their range extended an additional 10 km up the MF Eel River, to an apparent barrier (Figure 1). In the SF Eel River, squawfish extended their range 80 km by summer 1992 (M. Power personal communication). We observed range extensions on three occasions. In the MF Eel River, juvenile squawfish, about 100 mm SL, invaded previously unoccupied areas. In the Van Duzen River, larger adults invaded areas upstream of a high gradient area. Several larger squawfish were noted in the NF Eel River, 5 km upstream from the nearest conspecific fish.

Two larger streams, the Black Butte River and the NF Eel River, had not been extensively invaded during our study even though the warm, low gradient conditions seemed favorable. Neither stream had barriers to upstream dispersal in their lower reaches, but large deep pools were rare. The larger pools present had little cover. Large Sacramento suckers were also rare in these systems. The habitat requirements of large adults of these two species

are similar (Moyle 1976); thus, the low numbers of suckers in these streams may indicate that squawfish will never become abundant.

Sacramento squawfish have invaded some tributary streams but not others. We found juvenile squawfish in warm, low gradient tributaries some of which were intermittent during the summer. Squawfish were not found in cool, lower order streams. The continued absence of squawfish from cooler Eel River tributaries between Pillsbury Reservoir and Cape Horn Dam since their appearance in 1980 (P. Steiner unpublished data), suggests that this trend may hold over time throughout the drainage.

We first captured speckled dace in the Van Duzen River, 49 km above the confluence with the mainstem Eel River, during the summer of 1987. At that time their range only extended about 5 km downstream. The limited range of this species and the lack of records of its presence in the drainage indicated that it was introduced near the town of Bridgeville only a few years earlier. By 1989 they had extended their range five kilometers down-

Table 6. Results of canonical correlation analysis of the relative abundances of the six most common species with physical variables. Canonical loadings of the original variables on the first canonical factor derived from both fish relative abundances (FISH1) and physical factors (PHYS1) are given.

Fish species	FISH1	Physical variable	PHYS1
Rainbow trout	- 0.95	Order	0.85
Prickly sculpin	0.22	Water temperature	0.62
Threespine stickleback	0.55	Turbidity	0.67
Sacramento squawfish	0.57	Gradient	- 0.92
California roach	0.68	Elevation	- 0.62
Sacramento sucker	0.34	Average depth	0.61
		Maximum depth	0.65
		Width	0.82
		Fines	0.42
		Gravel	- 0.09
		Rubble	- 0.27
		Boulder	- 0.19
		Riffle	- 0.38
		Run	- 0.22
		Pool	0.39
		Surface turbulence	- 0.41
		Flow	0.70
		Attached algae	0.42

Wilks' lambda = 0.09, $F_{114,2171} = 10.09$, $p < 0.001$

Canonical correlation = 0.87

Canonical $r^2 = 0.76$

stream. The closest source population is the SF of the Trinity River, about 75 km away. Because speckled dace can tolerate a wide range of temperatures and prefer shallow riffles as habitat (Moyle 1976), we expect that their distribution will eventually include most of the Eel River drainage.

Fish assemblages and species-habitat relationships

We sampled 412 sites during the study but habitat data were analyzed from 401 sites, omitting sites in the estuary and sites for which some physical data were missing. Of the 17 species of fish observed in the drainage, only four native and two introduced species were common enough to be included in the PCA of fish relative abundances. Two PCs had eigenvalues greater than one. Together they accounted for 59% of the variance (Table 5). PC1 separated sites with high relative abundance of rainbow trout from sites characterized by high relative abundances of all the other species except prickly sculpin. The

second principal component separated the non-trout sites into two groups: (1) sites characterized by high relative abundance of California roach; and (2) sites characterized by high relative abundances of prickly sculpin, stickleback, and to a lesser extent Sacramento sucker. These results suggest three groupings of sites corresponding to species assemblages: (1) rainbow trout assemblage with rainbow trout relative abundance dominating all other species; (2) squawfish-roach assemblage characterized by high relative abundances of California roach and Sacramento squawfish and often associated with high relative abundances of Sacramento sucker and threespine stickleback; (3) California roach assemblage characterized by high relative abundances of California roach, low relative abundances of prickly sculpin, threespine stickleback, and sometimes Sacramento sucker.

Canonical correlation analysis of physical variables and fish relative abundances showed a strong correlation between physical conditions and co-occurrence of species (Table 6). The canonical load-

Table 7. Principal component loadings for the analysis of selected physical variables for sampling sites in the Eel River drainage (N = 401). Component loadings of less than 0.4 are indicated by an asterisk.

Physical variable	Component loadings				
	PC1	PC2	PC3	PC4	PC5
Order	0.85	*	*	*	*
Gradient (m km ⁻¹)	-0.78	*	*	*	*
Elevation (m)	*	*	0.61	*	*
Water temperature (°C)	0.61	*	*	*	*
Average depth (cm)	0.85	*	*	*	*
Maximum depth (cm)	0.86	*	*	*	*
Mean width (m)	0.90	*	*	*	*
Flow (m ³ sec ⁻¹)	0.76	0.40	*	*	*
Turbidity (1-5)	0.59	*	*	*	*
Shade (%)	-0.61	*	*	*	*
Attached algae (%)	0.40	*	*	*	-0.47
Fines (%)	0.52	*	*	*	*
Gravel (%)	*	*	*	-0.67	0.49
Rubble (%)	-0.52	0.40	*	*	*
Boulder (%)	*	*	0.85	*	*
Riffle (%)	-0.56	0.57	*	*	*
Run (%)	*	*	*	*	*
Pool (%)	0.62	-0.69	*	*	*
Surface turbulence (%)	-0.53	0.57	*	*	*
Percent of variance:	38.0	12.3	10.0	7.0	6.4
Cumulative variance:	38.0	50.3	60.3	67.3	73.7

ings of the original variables on the first canonical factors were very similar to the first principal components derived from the fish relative abundance and physical variables data sets (see below). The first canonical correlation explained 76% of the variance in the data set suggesting that the physical environment is a strong factor in determining relative abundances of fish species.

Principal components analysis of the physical variables produced five PCs with eigenvalues greater than one which explained 74% of the variance (Table 7). PC1 described a gradient ranging from small, clear, cool, shaded, rubble bottomed, high gradient, low order streams to large, turbid, warm, sand bottomed, low gradient, high order streams. PC2 separated sites dominated by pools from sites dominated by turbulent riffles. PC3 separated out high elevation sites with boulder and bedrock substrate from low elevation sites with finer substrates. PC4 separated sites on the basis of amount of gravel substrate. PC5 separated sites with high percentages of gravel and low percentages of attached algae from sites with large percentages of the bottom covered by attached algae and low percentages of gravel. The first two principal components explained the majority of the variance (50%).

Relative abundances of all six common species and total fish abundance exhibited statistically significant correlations with one or more of the physical PCs (Table 8). However, only correlations of rainbow trout, California roach and Sacramento squawfish relative abundances with PC1 were con-

sidered ecologically significant. Rainbow trout relative abundances were negatively correlated with physical PC1 indicating that rainbow trout dominated the fish assemblage in small, cold, high gradient tributaries and headwater streams (Table 8). California roach and Sacramento squawfish relative abundances were positively correlated with physical PC1 indicating that relative abundances of these species are highest in the warm, low gradient, habitats of the larger streams and rivers.

Discussion

Growth and diet of Sacramento squawfish

Successful invading species may show expanded trophic niches and accelerated growth rates when they first move into a new environment, because they take advantage of unexploited resources and inexperienced potential predators and competitors (Wikramanayake & Moyle 1989, Diamond & Case 1986, Werner 1986). Azuma (1992) found evidence for increased diet breadth in bluegills introduced into Japanese lakes. Wikramanayake & Moyle (1989) found that two of four species of fish (native to other Sri Lankan streams) introduced into naturally depauperate Sri Lankan streams grew to larger sizes than in their native streams. Nile perch, *Lates niloticus*, introduced into Lake Victoria about 1960 exhibited rapid growth in 1983 compared to populations in other African Lakes (Hughes 1992).

There was no evidence of increased diet breadth

Table 8. Correlations of total fish abundance (1–5) and individual species relative abundances with the principal components derived from the physical variables (N = 401). Correlations considered ecologically significant ($r \geq 0.45$) are underlined.

Species	PC1	PC2	PC3	PC4	PC5
Total abundance	0.21***	– 0.03	0.01	– 0.05	– 0.20***
Rainbow trout	<u>– 0.78***</u>	– 0.16**	0.09	0.04	0.16**
Prickly sculpin	– 0.01	0.33***	– 0.23***	0.25***	0.01
Threespine stickleback	0.31***	0.18***	– 0.39***	0.19***	– 0.19***
California roach	<u>0.60***</u>	– 0.01	0.07	– 0.15**	– 0.16**
Sacramento sucker	0.25***	0.14**	– 0.17**	0.11*	0.05
Sacramento squawfish	<u>0.49***</u>	0.19**	– 0.03	– 0.01	0.03

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

in the invading squawfish of the Eel River compared to a Sacramento River drainage population, although novel items were present in the diet (lamprey ammocoetes, amphibian larvae). This result was presumably related to the naturally broad diet of squawfish (Brown 1990). It may be unrealistic to expect evidence of increased diet breadth during introductions of generalized predators. The species composition of the Eel River at the time of squawfish introduction was comparable to that of many streams where squawfish are native. Increased diet breadth could have resulted if species richness had been higher in the Eel River. For example, the diet breadth of Nile perch introduced to Lake Victoria and other African lakes was likely much broader than in many other areas in Africa where the species is native, not because the diet expanded to include species previously used by other species but because the generalized diet included by default many new species not present in other areas (Goldschmidt et al. 1993, Hughes 1986, Ogutu-Ohwayo 1990). In Lake Victoria and Lake Kyoga, the initial broad diet breadth declined as previously abundant prey disappeared and the diet narrowed to three major prey, including juvenile Nile perch (Hughes 1986).

Increased growth is a more likely outcome if a similar predator is not already present. We did find evidence of increased growth in the first year of life in the SF Eel River, the most recently invaded area where we studied growth; however, there was no evidence for increased growth at any other life interval. Growth rates of Eel River squawfish were similar to those of squawfish in established populations in the native range of the species. In general, the biology of squawfish in the Eel River was very similar to that of native populations.

Status and distribution of native and introduced species

The Eel River has been regarded as one of the most productive salmon spawning streams in California, with the annual run of chinook salmon estimated at 103 000 fish and the annual run of coho salmon estimated at 42 000 fish as recently as 1980 (U.S. Heri-

tage and Conservation Service¹¹). All of the native anadromous fishes have declined in abundance (Table 1), including two to four species of salmon, two species of anadromous trout, a sturgeon, a stickleback and a smelt. Declines of salmon, trout and other species are not limited to the Eel River but have been noted throughout California (Brown et al. 1994, Moyle et al.³), and the entire Pacific Northwest region of North America (Nehlsen et al. 1991, Huntington et al. 1996). A variety of reasons are usually cited for declines in anadromous fish abundance but habitat degradation is one of the most common and is certainly important in the Eel River drainage.

The large scale removal of old growth forest on steep hillsides in the drainage in the decades following World War II, resulted in severe erosion and subsequent burying of the old stream channels with the eroded materials. The channels of the river and its major forks became shallower, braided, and less well defined (Lisle 1982). The exposed, shallow water presumably also became warmer during the summer months, making it less suitable for spawning and rearing of anadromous fishes (Kubicek 1977). Many of the smaller tributaries were less affected by (or recovered quickly from) these processes. These streams today have cool water, deep pools, and other characteristics favored by anadromous salmonids, especially if their watersheds remained at least partly forested. As a consequence, these streams are dominated by juvenile steelhead and coho salmon and usually lack invading species. It is likely that the conditions that now characterize these small tributaries were once more prevalent in the drainage and also characterized long reaches of the main channels as well.

Of the 16 fish species introduced into the drainage, ten are well established, the status of fathead minnow and white catfish is unknown, and four have not become established. In addition, threespine stickleback may have been introduced outside

¹¹ U.S. Heritage Conservation and Recreation Service. 1980. Final environmental impact statement, proposed designation of five California rivers in the national wild and scenic rivers system. U.S. Heritage and Conservation Service, Department of Interior, Washington, D.C. 322 pp.

their native range into the upper reaches of the drainage but these upstream populations, whether native or introduced, have declined or disappeared. The invading species, excluding threespine stickleback, form several distinct groups on the basis of life history or habitat use.

Two diadromous species have been introduced into the drainage, the ayu, which was intentionally introduced and the American shad, which invaded the system without human intervention after their original introduction into the Sacramento-San Joaquin River system. The ayu did not become established despite a significant attempt (Moyle 1976). The success of the shad may be partially explained by their temporal separation from the native anadromous salmonids. Shad use the mainstem Eel River during the spring for spawning and the summer for rearing, when anadromous salmonids are not abundant. The anadromous salmonids all spawn in fall and winter and either enter the ocean in the spring (chinook salmon) or favor the smaller, cooler tributary streams for rearing (rainbow trout, coho salmon, cutthroat trout).

The reason for the failure of the ayu is unknown but may be related to life history. Ayu are amphidromous and semelparous with an annual life cycle (McDowall 1988, Saruwatari 1995). The adults move downstream from August to November to spawn adhesive, demersal eggs on pebbles and stones. The embryos hatch from October to December and the larvae rear in the ocean from December to February. Juveniles move into the upper and middle reaches of rivers from January to April. Fall spawning may not be viable in the Eel River because of the high probability of high flows and associated substrate movements during the spawning and incubation times. It is also unknown whether the ocean currents at the mouth of the Eel River are favorable for retention of larvae.

The other three species that did not become established, brook charr, brown trout, and kokanee can be characterized as coldwater species introduced into inappropriate habitat. The failure of these introductions was likely because Pillsbury Reservoir, into which they were introduced, was too warm and anoxic in the summer (Fisk & Pelgren⁹, E. Ekman personal communication, B.

Bridges unpublished data). All three are widely established elsewhere in coldwater reservoirs (Moyle 1976).

Four of the established species can be grouped as successful in Pillsbury Reservoir but unsuccessful in the riverine portions of the drainage. Largemouth bass, bluegill, golden shiner, and threadfin shad, successful only in Pillsbury Reservoir, represent a variety of life history and trophic characteristics (Table 1). These species have not established populations in the rest of the drainage, even though individuals have been carried downstream with reservoir releases (Day⁷, R. Kruger unpublished data, P. Steiner unpublished data). All four species are basically adapted for living in lakes, ponds, or streams without extreme fluctuations in flow (Moyle 1976). For example, Meffe (1991) documented a failed invasion of a southeastern stream by bluegill at the same time they became successfully established in the reservoir that was the initial site of the introduction. The failure to establish a stream population was attributed to bluegill being poorly adapted for even low velocity stream habitat ($7\text{--}25\text{ cm sec}^{-1}$) and the presence of an intact native fish community. Slackwater habitat is common in the Eel River system during summer low flows but such habitat is rare during the winter and spring floods.

Green sunfish and brown bullhead have established populations in Pillsbury Reservoir and in the main river. The river populations are small and scattered. Both species can be described as warm water habitat generalists. Elsewhere in California, both species have been successful in small, warm streams as well as lentic habitats (Moyle 1976). Green sunfish have been particularly successful in Sierra Nevada foothill streams that are warm and intermittent during the summer, where they are often the dominant species (Moyle & Nichols 1973). They have likely not been more successful because of high flows and low temperatures during the fall, winter, and spring. Neither species has been notably successful in cold, large streams in other areas of California (Moyle 1976).

California roach, Sacramento squawfish, and speckled dace can be grouped as native California species introduced into areas outside of their native distributions. California roach and Sacramento

squawfish have clearly been successful invaders but the success of speckled dace is still in doubt. Each of the species is quite different from the others. Both roach and dace are small (70–80 mm SL as adults) cyprinids but the roach has a chunky, generalized, small-cyprinid morphology compared to the more flattened, streamlined morphology of the dace, which occupies faster water (Moyle 1976). Squawfish can reach 300–500 mm SL as adults and have the pike-like body shape characteristic of many piscivores (Moyle 1976). The squawfish is a carnivore, the roach is a detritivore/omnivore, and the speckled dace is an insectivore. The success of these species can be attributed to their demonstrated ability to handle the distinctive flow and temperature regimes of the regional rivers and not to any particular morphological or trophic attributes. California roach and Sacramento squawfish are native to the Russian River, the next large coastal system to the south of the Eel River (Moyle 1976). California roach are also native to several smaller coastal systems between the Russian and Eel Rivers (Moyle 1976). Speckled dace are native to coastal systems to the north (Klamath River) and south (Pajaro-Salinas River) of the Eel River (Moyle 1976).

Overall, it appears that the success or failure of an invading fish species in the Eel River has been mostly a function of the ability of the species to survive the fluctuating, highly seasonal, flow regime of the drainage. Interactions with native species appear to have had little effect on success or failure. However, the establishment of the present set of introduced species, especially predatory squawfish in the river and largemouth bass in the reservoir, may reduce the probability of additional species becoming established.

Fish assemblages and species-habitat relationships

The present group of six common resident species did exhibit patterns in relative abundances consistent with the existence of several different assemblages. On the basis of PCA (Table 5), three fish assemblages can be defined. The rainbow trout assemblage was characterized by high relative abundance of rainbow trout, dominating all other

species. The squawfish-roach assemblage was characterized by high relative abundances of California roach and Sacramento squawfish, often associated with high relative abundances of Sacramento sucker and threespine stickleback. The California roach assemblage was characterized by high relative abundance of California roach and low relative abundances (or absence) of prickly sculpin and threespine stickleback.

The CCA indicated that differences in assemblage structure among sites were associated with differences in physical habitat (Table 6). Correlations of individual species' relative abundances with physical habitat PC1 indicated that the responses of rainbow trout, California roach, and Sacramento squawfish were primarily responsible for the high canonical correlation (Table 8). Sites with the rainbow trout assemblage were generally on low order, low discharge, high gradient streams. These conditions were consistent with headwater and tributary streams. The other species dominated at high order, high discharge, low gradient sites, consistent with the larger rivers in the drainage. The squawfish-roach assemblage was characteristic of these sites. The roach assemblage was characteristic of sites in the mid-reaches of the rivers. Sacramento squawfish had not yet invaded these reaches, but physical conditions were too stressful for trout. These sites were also upstream of the areas where threespine stickleback and prickly sculpin were common. Sites on the lower portions of the North Fork Eel River and Black Butte River were good examples.

We do not believe these assemblages will persist for a number of reasons. First, the squawfish population was still expanding at the time of our study and consequently the effects of squawfish predation have not been realized throughout the drainage. Almost by definition, successful invaders will change the biotic environment they invade (e.g. Mooney & Drake 1986, Drake et al. 1989). The invasion of squawfish into the Eel has caused major shifts in how the established species use the available habitat and has increased the likelihood of competitive interactions among them (Brown & Moyle 1991, Brown & Brasher 1995). Experimental studies (L. Brown & A. Brasher unpublished data)

indicated that threespine sticklebacks were exceptionally vulnerable to squawfish predation in areas, such as the Eel River, where cover is sparse. Those results supported the field observations of Smith (1982) that squawfish and sticklebacks do not coexist in pools with sparse cover. Thus, it seems likely that population densities and the range of stickleback in the drainage will be reduced because cover is scarce in many areas. Extirpation of this species in much or all of the drainage is possible.

Second, within their native ranges, Sacramento squawfish and California roach generally do not exhibit a strong positive association, presumably due to predation by squawfish (Moyle & Nichols 1973, Moyle & Daniels 1982, Smith 1982, Brown & Moyle 1993). Sacramento squawfish is typically part of an assemblage that includes Sacramento sucker and hardhead, *Mylopharodon conocephalus*, a large cyprinid. This assemblage is characteristic of relatively large streams with low summer discharges and high summertime temperatures (Moyle & Nichols 1973, Brown & Moyle 1993). California roach is sometimes associated with this assemblage but form a separate single-species assemblage characteristically found in small, warm, often intermittent streams. It seems likely that the strong association of California roach and Sacramento squawfish in the Eel River will eventually weaken and the species become more segregated.

Third, the status of speckled dace as a successful or unsuccessful invader has not yet been established. Speckled dace could establish large populations in riffle habitat particularly in upstream areas where sculpins are now rare or absent.

Fourth, populations of anadromous fishes are at record low levels as a result of conditions in the drainage combined with outside factors such as fishing and unfavorable oceanic conditions (Moyle et al.³, Brown et al. 1994). Juvenile coho salmon spend the first year or so in cool streams. If coho salmon populations recover, juveniles will become an important component of the resident fish fauna. Coastal cutthroat trout might also become an important species in the lower part of the drainage.

Speculation for the future

The overall effect of the successful introductions of species into the Eel River drainage has been to assemble a group of species, with some exceptions, that naturally occur together in many California streams (Moyle & Nichols 1973, Moyle & Daniels 1982, Smith 1982, Taylor et al. 1982, Brown & Moyle 1993). These species appear to be organizing into assemblages similar to those found in other California streams. An important factor contributing to this process is the similarity of the physical habitat in the Eel River to that found in other parts of California. For example, physiological and behavioral responses of the species to temperature are strong organizational forces in native California stream fish assemblages (Baltz et al. 1982, Baltz et al. 1987, Cech et al. 1990).

Barring new introductions, we expect that four habitat-associated assemblages will develop: (1) Squawfish-sucker assemblage; (2) roach assemblage; (3) coho-rainbow trout assemblage; and (4) headwater rainbow trout assemblage. The squawfish-sucker assemblage is analogous to the squawfish-sucker-hardhead assemblage, the highly structured assemblage found in many of the larger streams of the Sacramento-San Joaquin drainage (Moyle & Nichols 1973, Baltz & Moyle 1993, Brown & Moyle 1993). It is now developing in the warmer reaches of the main channels of the Eel and its larger tributaries. Eventually, it will have squawfish and suckers dominating pools and runs, and sculpins, trout, and perhaps speckled dace dominating the riffles. California roach will still be present but will be less dominant than they are presently. The presence of trout will depend on water temperatures; during drought years flows may be too low and temperatures too high to support them (Kubicek 1977). The presence of coastrange sculpin will depend on distance of from the estuary because their presence in upstream areas depends on dispersal from the lower river (Brown et al. 1995). In the Sacramento-San Joaquin drainage, the sculpin present in the assemblage is the riffle sculpin, *Cottus gulosus*. The presence of both coastrange and prickly sculpin in the new Eel River assemblage will add a new level of complexity to the riffle portion of

the assemblage. Ecological differences between the species are minor and how they manage to coexist is not known although they are common companion species in Pacific coast streams (Brown et al. 1995).

The roach assemblage will consist primarily of roach, with small numbers of juvenile suckers and squawfish in small, warm, low-gradient tributaries to the main channels. A similar assemblage exists in the Sacramento-San Joaquin drainage (Moyle & Nichols 1973, Moyle 1976, Brown & Moyle 1993).

The coho-rainbow trout assemblage exists today in the more heavily forested tributaries, where large woody debris, heavy shade, and cold water create conditions optimal for the rearing of both juvenile coho salmon and rainbow trout. However, coho salmon populations have been at low levels in recent years (Brown et al. 1994), so the importance of this assemblage will depend on how well salmon populations recover. Either or both species of sculpins are frequently present in these streams as well, depending on their location.

The headwater rainbow trout assemblage is widespread in the smaller, high gradient tributaries where rainbow trout is the only species present and there is a lack of deep pools and colder temperatures favored by coho salmon. A special situation exists in the uppermost reaches of the MF and the Van Duzen River, where 'summer' steelhead are present. Adult summer steelhead ascend the rivers to these reaches in the spring, spend the summer there in deep pools and then spawn in the fall, with the juveniles spending 1–2 years in the streams before going out to sea.

The squawfish-sucker-hardhead assemblage is very resistant to introduction of exotic species in the absence of human caused habitat modifications (Baltz & Moyle 1993); therefore, success of new introductions in the Eel River may be less likely than in the past, in areas where the squawfish-sucker assemblage becomes established. Results from field, laboratory, and simulation studies of community assemblage indicate that the order of invasion, rate of invasion, and the presence of predators can be very important to the final outcome (Post & Pimm 1983, Alford & Wilbur 1985, Wilbur & Alford 1985, Gilpin et al. 1986, Robinson & Dickerson 1987, Robinson & Edgemon 1988, Drake 1990, Drake 1991,

Moyle & Light 1996b). The similarity of the species composition of the present assemblage community to fish assemblages found in other California streams may also explain why the effects of the squawfish introduction have been relatively modest compared to the effects introduced predators have had in some other systems (e.g., Zaret & Paine 1973, Goldschmidt et al. 1993).

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