

Segregation by species and size classes of rainbow trout, *Salmo gairdneri*, and Sacramento sucker, *Catostomus occidentalis*, in three California streams

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Keywords: Competition, Microhabitat, Overlap, Stream temperature

Synopsis

The hypothesis that Sacramento suckers, *Catostomus occidentalis*, compete with rainbow trout, *Salmo gairdneri*, for space in streams was examined by measuring microhabitat utilization of both species in three California streams. Two streams were similar in most respects except one contained only trout and one contained trout and a large population of suckers. The third stream, formed by the union of the first two, contained trout and a small population of suckers. The species overlapped in five of the six microhabitat variables measured: maximum depth, mean water column velocity, focal point velocity, surface water velocity, and substrate type. However, the species had strong vertical segregation; there was little overlap between species in focal point depth. Mean focal point velocities were also significantly different. Suckers roamed over and generally remained in contact with the bottom while trout held position in the water column. Microhabitat utilization by trout in the stream without suckers was similar to in the stream with a higher sucker density. Differences in microhabitat utilization by trout between the third stream and the other two was attributed to the larger size of the third stream. Both sucker and trout showed a similar within-species segregation of size classes — fish under 50 mm in length sought shallow water. Size-specific trends indicated ontogenic shifts in resource utilization which reduced overlap within species. These results suggest that competition for space between trout and suckers was not a major factor regulating microhabitat utilization of trout, although the possibility that larger suckers may displace small trout needs further study.

Introduction

Competition for food and space is widely considered to be a major factor structuring assemblages of stream fishes (Grossman et al. 1982), although studies that clearly demonstrate its importance are few (Baltz et al. 1982). In particular, competition from nongame fishes is frequently given as a major cause of the decline of gamefish (mostly trout) densities in streams, especially populations of salmonids (Eschmeyer 1975). Recent reviews (Moyle 1977, Holey et al. 1979, Brown & Moyle 1981)

demonstrate that there is little evidence to support this supposition and that most declines in gamefish are caused by overfishing or by changes in environmental conditions that coincidentally favor nongame species. Changes in temperature regime are particularly likely to be important in this regard (Baltz et al. 1982). Nevertheless, managers of trout and salmon streams spend considerable time and effort attempting to reduce nongame fish densities in streams, especially through the use of poisons (Eschmeyer 1975, Moyle et al. 1983). In the western United States, much of this management effort

focuses on suckers, *Catostomus* spp., although their interactions with trout (mainly *Salmo* spp.) are poorly understood. Most studies show that dietary overlap between suckers and trout is minimal (Ashley 1974, Moyle 1976, Li & Moyle 1976, Holey et al. 1979, Marrin & Erman 1982), so if direct competition is occurring between species, it is most likely for space. Therefore, the purpose of this study was to compare microhabitats of various size classes of rainbow trout, *S. gairdneri*, and Sacramento sucker, *C. occidentalis*, in three reaches of a Sierra Nevada stream system to determine if the species and size classes were ecologically segregated and if presence of suckers affected microhabitat utilization by trout.

Materials and methods

Study area. — We collected microhabitat utilization data on rainbow trout and Sacramento suckers in three reaches of two confluent streams near the northwestern border of Yosemite National Park, California. One study reach was located on Eleanor Creek below Eleanor Reservoir. Two study reaches were located on Cherry Creek: one below Lloyd Reservoir and another 7 km downstream below the confluence of Cherry and Eleanor creeks. Cherry and Eleanor creeks were similar in morphology above their confluence although Cherry Creek possessed more area of gravel riffle. Flow regimes were also similar and regulated by dams; however, the sources of discharge from the dams caused temperature differences between streams. Discharge from Eleanor Reservoir was from the epilimnion while discharge from Lloyd Reservoir was from the hypolimnion. Ryan model J thermographs recorded daily variation in stream temperature between 17 June and 16 October 1981. Discharge from Lloyd Reservoir was $5 \text{ m}^3 \text{ min}^{-1}$ (5–6 cfs) from 31 May to 30 June 1981. Eleanor Reservoir spilled over from 31 May to 15 June and discharge ranged from 90 to $610 \text{ m}^3 \text{ min}^{-1}$ (53–359 cfs), but was reduced to $5 \text{ m}^3 \text{ min}^{-1}$ (5–6 cfs) from 16–30 June 1981. With minor exceptions discharge from both dams was maintained at $28 \text{ m}^3 \text{ min}^{-1}$ (15–18 cfs) between 1 July and 1 October 1981. Below the confluence, flow in lower

Cherry Creek was approximately the sum of the releases from Eleanor and Lloyd Reservoirs. In appearance the three sites were similar, as the reaches flowed over boulder and bedrock substrates, through steep canyons. Riparian vegetation was scant and pools were common, although the largest and deepest pools were found in lower Cherry Creek, where flows were greatest.

Microhabitat analysis. — Fish were located by observers snorkeling in an upstream direction. Some measurements of trout alevins and sucker young-of-year (Y-O-Y) were made along the stream edge by observers standing on the stream bank. Once fish were located, the following data were recorded: (1) water velocity at the place the fish was located (i.e. focal point velocity), (2) mean water column velocity, (3) surface water velocity, (4) distance of fish from bottom (i.e. focal point depth), (5) maximum depth of water column, (6) substrate below fish, (7) number of individuals, and (8) the estimated length of fish. The measurements reported here are for independent observations on one or more fish, and repeated observations on the same individual were avoided by systematically sampling sections of stream only once and in an upstream direction. Between 1 July and 20 August 1981 we spent 15 days making 1636 independent microhabitat observations on a total of 2621 fishes. We made 1072 independent observations on 1568 trout and 564 independent observations on 1053 suckers.

Velocity and depth measurements were made with a Marsh-McBirney electronic flow meter mounted on a top-setting wading rod. When the water depth exceeded 0.75 m or the water column was obstructed, mean water column velocity was calculated using velocities taken at proportional depths of 0.2, 0.6 and 0.8 of the water column. Otherwise only the velocity at the proportional depth of 0.6 was used (Bovee & Milhous 1978). The substrate composition was estimated using a modified Wentworth particle size scale (Bovee & Cochran 1977). Water column depth and focal point depth were read directly on the wading rod. Length of fish was estimated by comparison with substrate elements which in turn were measured with wading rod. Since we were interested in the effects of size on

resource use and overlap, the measurements on both species were stratified by reach and size class for statistical comparisons. Individuals less than or equal to 50 mm standard length (SL) were grouped as Y-O-Y, individuals 51 to 119 mm SL were grouped as juveniles, and individuals greater than or equal to 120 mm SL were grouped as adults. These size categories were equivalent to the age categories of young-of-year, yearling, and fish of age two or older (Snider & Linden 1981).

Microhabitat variables were compared within species in a two-way analysis of variance (ANOVA) using size class and site as fixed factors. Between-species comparisons were made by combining all sites using species and size class as fixed factors. The Rummage statistical package (Bryce 1980) was used for ANOVA and Bonferonni's posterior test. Microhabitat utilization data were transformed ($\log_{10} X + 1$) to satisfy the normality and equal variance

assumptions of ANOVA. Statistical tests reported for these variables are from transformed data, but means and distributions are not scaled. The utilization by fish of the deepest pools (> 1.2 m) in some study sections positively skewed the variable distributions for maximum depth and focal point depth and hence over emphasized differences in variance among sites in the two-way ANOVA. Therefore, such observations were omitted from the analysis as were outliers for other microhabitat variables.

Overlap in microhabitat utilization was calculated using Schoener's (1970) formula and the pooled distributions presented for each size class.

Results

Stream temperature

Daily minimum and maximum temperatures for the three study sites indicated substantial differences among reaches during summer months (Fig. 1). For the period of August 20, through October 30, 1981, the mean daily maxima were ($\bar{x} \pm \text{SD}$, $N = 42$) 20.7 ± 1.69 , 13.2 ± 2.13 , and $17.3 \pm 1.67^\circ\text{C}$ for Eleanor, upper Cherry, and lower Cherry creeks, respectively. While the mean diel variations were 1.5 ± 0.24 , 4.8 ± 1.00 and $1.0 \pm 0.29^\circ\text{C}$, respectively. Stream temperatures in Eleanor Creek were higher but less variable than in upper Cherry Creek. Stream temperatures in lower Cherry Creek, below the confluence, generally paralleled those in Eleanor Creek but at a lower level and with less diel variation.

Distribution and growth

Rainbow trout were present in all three study sites, but sacramento suckers were absent from the upper Cherry Creek site even though they were present in Lloyd Lake above the site and in lower Cherry Creek, below the confluence. We observed green sunfish, *Lepomis cyanellus*, on seven occasions in Eleanor Creek but no other fishes were present in the study streams. Electrofishing estimates using a three pass depletion technique with block nets indicated that there were approximately 11 suckers

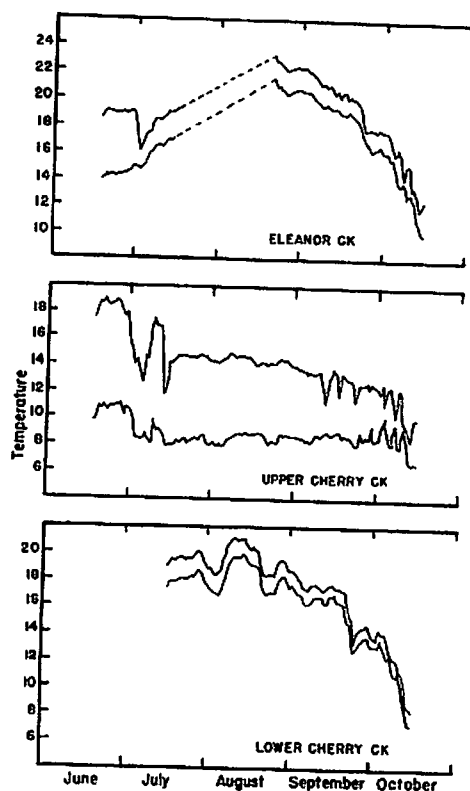


Fig. 1. Daily minimum and maximum water temperatures ($^\circ\text{C}$) at three study sites in the western Sierra Nevada near Yosemite National Park.

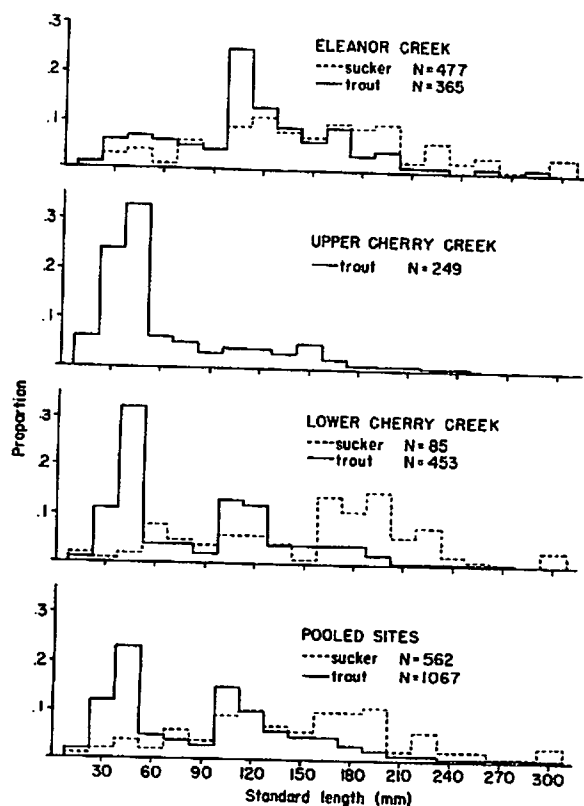


Fig. 2. The length frequency of rainbow trout and Sacramento sucker in three study sites. Suckers were absent from the upper Cherry Creek reach.

per 100 m² of stream in Eleanor Creek, while snorkeling surveys with three observers indicated only 2 suckers per 100 m² of stream in lower Cherry Creek (Moyle & Baltz unpublished data). Abundance estimates for trout greater than 50 mm SL in Eleanor, upper Cherry, and lower Cherry creeks were 10, 10 and 12 per 100 m², respectively. Estimates for trout less than 50 mm SL were 1, 24 and 6 fish per 100 m² in Eleanor, upper Cherry, and lower Cherry creeks, respectively. The differences in densities of trout Y-O-Y among reaches were related to the greater availability of rearing habitat in Cherry Creek (Baltz & Moyle unpublished data). Electrofishing was inefficient in these reaches due to low conductivity, thus our estimates only provided a ranking of the relative abundances of species in each section. The size distributions of both species in each site (Fig. 2) are typical of many California

streams (Moyle 1976). Limited growth data on rainbow trout in Eleanor Creek indicated slow growth compared to other Sierra Nevada populations (Snider & Linden 1981). Size distributions of trout at the other study reaches were similar (Fig. 2) so growth rates were presumably similar as well. Lengths for suckers in Eleanor Creek were 82, 123, 156 and 183 mm SL at ages one through four, respectively and are low compared to other populations (Burns 1966, Moyle et al. 1983, N. Villa, personal communication).

Microhabitat utilization

Maximum depth. — In a two-way ANOVA, the maximum depth utilized by rainbow trout differed significantly by size class (F-ratio = 145.9; df = 2, 1038; $P < 0.001$) and site (F-ratio = 18.9; df = 2, 1038; $P < 0.001$). Larger trout utilized deeper water (Table 1) but pairwise comparisons indicated that juvenile and adult classes utilized depths that were not significantly different ($P > 0.05$), while Y-O-Y differed significantly from other classes ($P < 0.05$). Site differences for trout were only significant between reaches on Cherry Creek ($P < 0.05$). The maximum depth utilized by Sacramento suckers differed significantly among size classes (F-ratio = 24.8; df = 2, 543; $P < 0.001$) and between sites (F-ratio = 4.9; df = 1, 543; $P < 0.03$). Sucker Y-O-Y used significantly shallower water than did juveniles

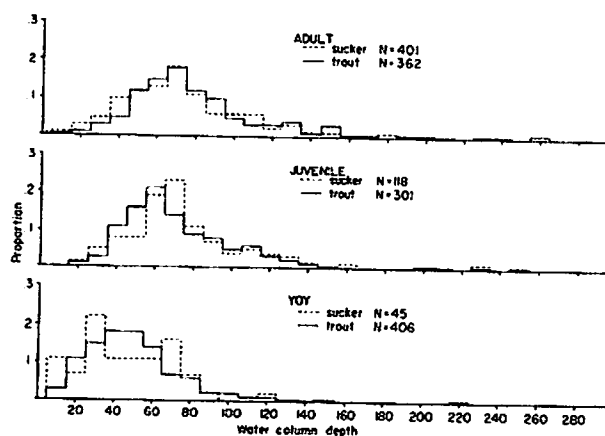


Fig. 3. The maximum depth (cm) utilized by rainbow trout and Sacramento sucker in three sites. Data from sites are pooled.

Table 1. Means of microhabitat variables for size classes of rainbow trout and Sacramento sucker in three western Sierra Nevada stream reaches. Figures are means \pm standard deviation (sample size) and units are centimeters for depths and centimeters \cdot sec⁻¹ for velocities. See Fig. 7 for explanation of substrate types.

	Cherry Creek		Eleanor Creek	Pooled sites
	Lower reach	Upper reach		
<i>Maximum depth¹</i>				
Rainbow trout				
Y-O-Y	58.2 ± 29.3 (199)	39.7 ± 20.5 (155)	50.6 ± 20.1 (50)	50.2 ± 26.6 (406)
Juvenile	71.9 ± 31.1 (108)	78.2 ± 31.4 (46)	70.7 ± 30.8 (147)	72.3 ± 31.0 (301)
Adult	79.9 ± 32.7 (146)	83.8 ± 36.1 (47)	81.6 ± 45.9 (168)	81.1 ± 40.0 (362)
Sacramento sucker				
Y-O-Y	48.0 ± 34.9 (5)	—	46.6 ± 24.5 (40)	46.7 ± 25.3 (45)
Juvenile	88.8 ± 49.0 (19)	—	71.0 ± 23.9 (99)	73.9 ± 29.9 (118)
Adult	78.3 ± 29.3 (61)	—	71.1 ± 31.1 (338)	72.1 ± 30.9 (401)
<i>Focal point depth²</i>				
Rainbow trout				
Y-O-Y	9.5 ± 10.1 (199)	3.5 ± 5.1 (156)	11.8 ± 9.0 (50)	7.5 ± 9.0 (407)
Juvenile	18.0 ± 20.0 (108)	13.5 ± 14.2 (46)	24.0 ± 22.3 (147)	20.2 ± 20.7 (302)
Adult	24.6 ± 18.2 (146)	18.4 ± 17.6 (47)	30.6 ± 36.0 (168)	26.5 ± 28.1 (362)
Sacramento sucker				
Y-O-Y	0.4 ± 0.9 (5)	—	0.9 ± 2.4 (40)	0.8 ± 2.3 (45)
Juvenile	8.2 ± 22.2 (19)	—	2.2 ± 13.9 (99)	3.1 ± 15.6 (118)
Adult	0.9 ± 5.2 (61)	—	1.7 ± 10.5 (338)	1.8 ± 10.2 (401)
<i>Mean water column velocity³</i>				
Rainbow trout				
Y-O-Y	10.3 ± 11.7 (199)	12.3 ± 10.3 (155)	12.6 ± 12.2 (50)	11.3 ± 11.3 (406)
Juvenile	14.9 ± 18.9 (107)	12.2 ± 8.9 (46)	13.8 ± 13.1 (147)	13.9 ± 14.9 (302)
Adult	14.7 ± 12.6 (146)	14.8 ± 16.6 (47)	17.1 ± 15.4 (167)	15.8 ± 14.5 (361)
Sacramento sucker				
Y-O-Y	3.2 ± 1.3 (5)	—	7.7 ± 10.4 (40)	7.2 ± 9.9 (45)
Juvenile	13.0 ± 8.5 (19)	—	10.7 ± 10.0 (97)	11.1 ± 9.8 (116)
Adult	22.6 ± 27.0 (61)	—	14.3 ± 15.3 (336)	15.5 ± 17.7 (399)
<i>Focal point velocity</i>				
Rainbow trout				
Y-O-Y	7.0 ± 7.1 (199)	7.5 ± 7.4 (156)	10.3 ± 12.2 (50)	7.5 ± 8.1 (407)
Juvenile	10.8 ± 11.1 (108)	10.2 ± 8.2 (46)	11.5 ± 9.9 (146)	11.1 ± 10.0 (302)
Adult	12.6 ± 11.0 (146)	13.3 ± 10.4 (47)	15.7 ± 12.6 (168)	14.2 ± 11.8 (362)
Sacramento sucker				
Y-O-Y	2.6 ± 1.5 (5)	—	4.1 ± 5.6 (40)	3.9 ± 5.3 (45)
Juvenile	6.0 ± 5.3 (19)	—	7.5 ± 8.4 (99)	7.3 ± 8.0 (118)
Adult	11.5 ± 15.2 (61)	—	9.2 ± 11.4 (336)	9.6 ± 12.0 (399)
<i>Surface water velocity</i>				
Rainbow trout				
Y-O-Y	17.9 ± 15.0 (199)	16.0 ± 12.5 (156)	21.1 ± 20.0 (50)	17.5 ± 14.9 (407)
Juvenile	22.9 ± 20.6 (108)	15.3 ± 12.6 (46)	24.2 ± 19.9 (147)	22.4 ± 19.4 (303)
Adult	28.0 ± 21.8 (146)	19.7 ± 20.2 (46)	24.8 ± 17.5 (168)	25.4 ± 19.8 (361)
Sacramento sucker				
Y-O-Y	5.2 ± 2.2 (5)	—	11.3 ± 11.0 (40)	10.6 ± 10.6 (45)
Juvenile	17.2 ± 9.4 (19)	—	16.2 ± 15.4 (99)	16.4 ± 14.6 (118)
Adult	35.8 ± 30.0 (61)	—	23.3 ± 19.9 (338)	25.3 ± 22.1 (401)

Table 1. Cont.

Substrate type				
Rainbow trout				
Y-O-Y	6.8 ± 0.9 (199)	6.3 ± 1.0 (155)	7.0 ± 0.8 (50)	6.6 ± 1.0 (406)
Juvenile	6.8 ± 0.9 (108)	6.9 ± 1.4 (46)	7.2 ± 0.8 (147)	7.0 ± 0.9 (303)
Adult	7.0 ± 0.7 (145)	7.0 ± 1.3 (47)	7.3 ± 0.6 (168)	7.1 ± 0.8 (361)
Sacramento sucker				
Y-O-Y	6.8 ± 1.6 (5)	—	7.2 ± 0.8 (40)	7.2 ± 0.9 (45)
Juvenile	7.0 ± 0.9 (19)	—	7.1 ± 0.9 (99)	7.1 ± 0.9 (118)
Adult	7.0 ± 1.4 (61)	—	7.3 ± 0.8 (338)	7.2 ± 0.9 (401)

¹ Values > 161 cm were excluded from ANOVA

² Values > 121 cm were excluded from ANOVA.

³ Values > 75 cm · s⁻¹ were excluded from ANOVA

and adults ($P < 0.05$) but means for juveniles and adults (Table 1) did not differ. In a nested analysis of variance with species and size class as fixed factors, posterior testing indicated no pairwise difference between equivalent size classes (Fig. 3) for Y-O-Y and juveniles ($P > 0.05$) of suckers and trout but adult trout used deeper water than did adult suckers ($P < 0.05$). Index values for interspecific overlap of maximum depth were generally high (Table 2).

Focal point depth. — The focal point depth of rainbow trout differed significantly by size class (F-ratio = 250.1; $df = 2$, 1050; $P < 0.001$) and site (F-ratio = 58.2; $df = 2$, 1050; $P < 0.001$). Means (Table 1) increased with trout size and pairwise comparisons indicated that all size classes and sites differed significantly ($P < 0.05$). The focal point depth of Sacramento suckers differed significantly among size classes (F-ratio = 3.8; $df = 2$, 543; $P < 0.05$) but site differences were not significant (F-ratio = 0.2; $df = 1$, 543; $P > 0.66$). All sucker size classes (Table 1) differed significantly in pairwise comparisons ($P < 0.05$). Between species all equivalent size classes (Fig. 4) were significantly different ($P < 0.05$) and trout were always higher in the water column than were the equivalent size classes of suckers. Interspecific overlap in focal point depth was generally low but trout Y-O-Y had moderately high overlap with all sucker size classes, while suckers and other trout size classes partitioned the water column vertically (Table 2).

Mean water column velocity. — The mean water column velocity utilized by rainbow trout differed significantly by size class (F-ratio = 12.1; $df = 2$, 1050; $P < 0.001$) and site (F-ratio = 3.2; $df = 2$, 1050; $P < 0.05$). Means (Table 1) increased with trout size but pairwise comparisons indicated a significant difference only between Y-O-Y and adults ($P < 0.05$) and by site only between lower

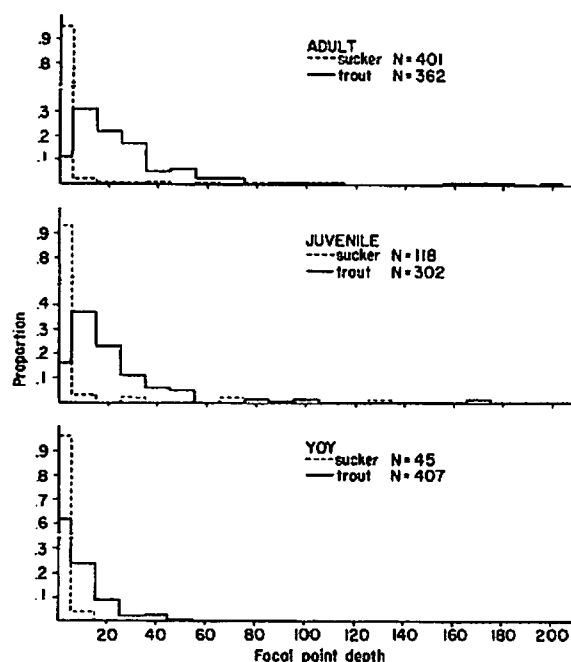


Fig. 4. The focal point depth (cm) utilized by rainbow trout and Sacramento sucker in three sites. Data from sites are pooled.

Table 2. Interspecific values of Schoener's (1970) index of overlap in microhabitat variables among size classes of rainbow trout and Sacramento sucker.

Microhabitat variable	Sacramento sucker	Rainbow trout		
		Y-O-Y	Juvenile	Adult
Maximum depth	Y-O-Y	0.74	0.62	0.58
	Juvenile	0.74	0.84	0.83
	Adult	0.64	0.85	0.85
Focal point depth	Y-O-Y	0.66	0.20	0.20
	Juvenile	0.67	0.21	0.16
	Adult	0.66	0.20	0.15
Mean water column velocity	Y-O-Y	0.68	0.62	0.63
	Juvenile	0.90	0.86	0.83
	Adult	0.90	0.85	0.92
Focal point velocity	Y-O-Y	0.78	0.63	0.53
	Juvenile	0.97	0.83	0.73
	Adult	0.92	0.70	0.72
Surface water velocity	Y-O-Y	0.77	0.71	0.70
	Juvenile	0.92	0.83	0.80
	Adult	0.83	0.81	0.90
Substrate type	Y-O-Y	0.68	0.81	0.86
	Juvenile	0.75	0.89	0.92
	Adult	0.73	0.88	0.93

Cherry and Eleanor creeks ($P < 0.05$). The mean water column velocity utilized by Sacramento suckers differed significantly among size classes (F-ratio = 16.7; $df = 2, 543$; $P < 0.001$) and between sites (F-ratio = 4.1; $df = 1, 543$; $P < 0.05$). Mean water column velocities (Table 1) increased with size class but only Y-O-Y were significantly different ($P < 0.05$). Between species comparisons of equivalent size classes (Fig. 5) indicated that Y-O-Y were significantly different ($P < 0.05$) but juveniles and adults were not different. Interspecific overlap was generally very high; however, trout only overlapped moderately with sucker Y-O-Y (Table 2).

Focal point velocities. — The focal point velocities differed significantly by size class (F-ratio = 38.9; $df = 2, 1057$; $P < 0.001$) and site (F-ratio = 5.0; $df = 2, 1057$; $P < 0.01$) for rainbow trout. Mean (Table 1) velocities increased with trout size and pairwise comparison indicated that all size classes

were different ($P < 0.05$) but only the lower Cherry and Eleanor creek sites differed ($P < 0.05$). The focal point velocities of Sacramento suckers differed significantly among size classes (F-ratio = 8.1; $df = 2, 543$; $P < 0.001$) but not between sites (F-ratio = 0.8; $df = 1, 543$; $P > 0.35$). Focal point velocity increased with sucker size (Table 1) but pairwise comparisons were not significant between adjacent size classes, only between Y-O-Y and adult ($P < 0.05$). Between species all equivalent size classes were significantly different ($P < 0.05$) and mean focal point velocities were always higher for trout size classes (Fig. 6). Interspecific overlap in focal point velocity was moderate to high but trout Y-O-Y had very high overlap with juvenile and adult suckers (Table 2).

Surface water velocity. — The surface water velocity over rainbow trout differed among size classes (F-ratio = 19.0; $df = 2, 1057$; $P < 0.001$) and sites (F-ratio = 6.9; $df = 2, 1057$; $P < 0.001$). Means (Table 1) increased with trout size but differences were significant only between Y-O-Y and adults ($P < 0.05$). Site differences were significant ($P < 0.05$) except

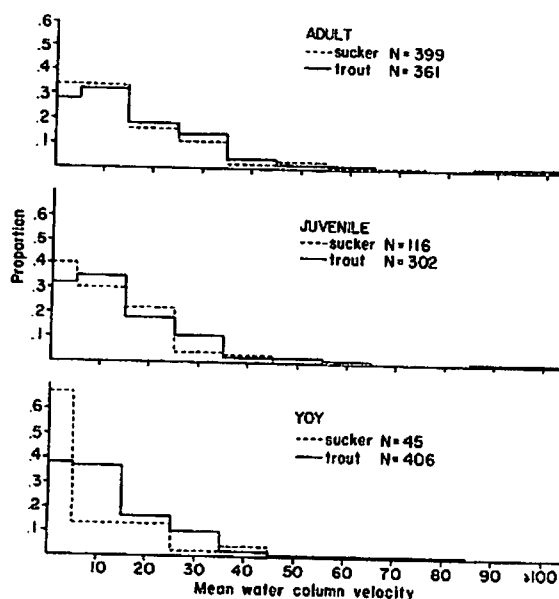


Fig. 5. The mean water column velocities ($\text{cm} \cdot \text{s}^{-1}$) utilized by rainbow trout and Sacramento sucker in three sites. Data from sites are pooled.

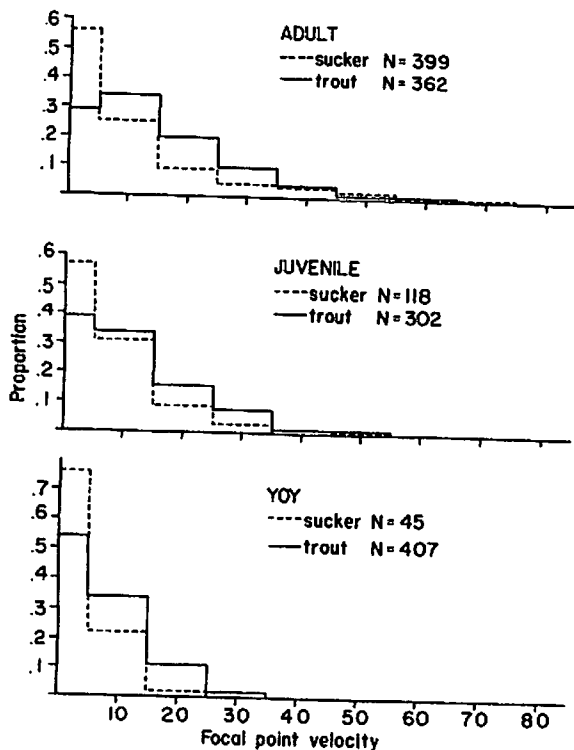


Fig. 6. The focal point velocities ($\text{cm} \cdot \text{s}^{-1}$) utilized by rainbow trout and Sacramento sucker in three sites. Data from sites are pooled.

between lower Cherry and Eleanor creeks. For Sacramento suckers, surface water velocity differed significantly among size classes ($F\text{-ratio} = 16.5$; $df = 2, 543$; $P < 0.001$) and between sites ($F\text{-ratio} = 6.5$; $df = 1, 543$; $P < 0.02$). Mean velocities (Table 1) increased with sucker size and all pairwise comparisons were significantly different ($P < 0.05$). Between species comparisons of equivalent size classes indicated that trout Y-O-Y and juveniles were found under significantly faster surface water velocities than were sucker Y-O-Y ($P < 0.05$) and juveniles ($P < 0.05$) but adult differences were not significant ($P > 0.05$). Interspecific overlap was generally high (Table 2).

Substrate. — The substrate utilized by rainbow trout differed significantly among size classes ($F\text{-ratio} = 28.0$; $df = 2, 1056$; $P < 0.001$) and sites ($F\text{-ratio} = 25.8$; $df = 2, 1056$; $P < 0.001$). Pairwise comparisons indicated significant differences ($P < 0.05$)

except between juveniles and adults, and all sites were different ($P < 0.05$). The substrate utilized by sacramento suckers did not differ among size classes ($F\text{-ratio} = 0.5$; $df = 2, 543$; $P > 0.58$) but sites were different ($F\text{-ratio} = 10.2$; $df = 1, 543$; $P < 0.02$). Between species comparisons of equivalent size classes (Fig. 7) indicated that Y-O-Y and juveniles were significantly different ($P < 0.05$) but juveniles and adults were not different. Since the substrate composition was largely boulder and bedrock in the three study reaches, overlap in utilization was very high (Tables 2 and 3).

Ontogeny and intraspecific overlap

Both species showed size-related differences in microhabitat use, with the values of most microhabitat variables increasing as length increased (Table 1). Rainbow trout Y-O-Y and adult size classes showed less overlap than did either size class with juveniles, indicating that intraspecific overlap was reduced by ontogenic shifts in space utilization (Table 3). However, there was no clear pattern for

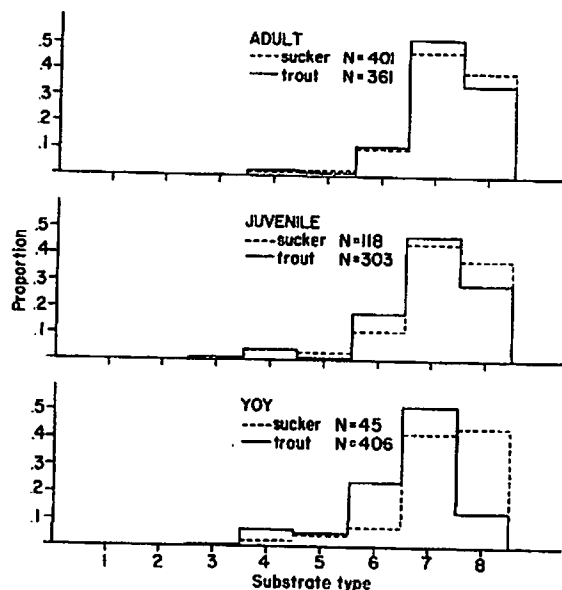


Fig. 7. Substrates utilized by rainbow trout and Sacramento sucker in three sites. Substrate types are: 1 = plant detritus, 2 = silt, 3 = mud, 4 = sand, 5 = gravel, 6 = cobble, 7 = boulder and 8 = bedrock (Bovee & Cochnauer 1977).

Sacramento sucker size classes (Table 3), although sucker Y-O-Y were concentrated along the stream edge.

Discussion

Differences in microhabitat utilization by rainbow trout were found among sites, but most differences were between the lower Cherry Creek reach, where flows were highest, and the upper reaches. No differences were found between the two upper reaches in maximum depth utilized, mean water column velocity, and focal point velocity, although upper Cherry Creek contained only rainbow trout, while Eleanor Creek contained large stocks of both suckers and trout. Trout in Eleanor Creek did have higher focal point depths which may reflect displacement by suckers. However, if suckers were displacing trout from favored microhabitats in Eleanor Creek we would expect that the trout would be displaced to areas of higher velocity, where it is energetically more expensive to obtain favored food organisms (Smith & Li 1983). Higher temperatures should have a similar effect, as Smith & Li (1983) found that juvenile rainbow trout sought higher focal point velocities at higher temperatures in California coastal streams. Thus the evidence suggests that trout use similar microhabitats whether or not suckers are present, within the temperature ranges encountered in Cherry and Eleanor creeks. The apparent unimportance of stream temperatures in determining microhabitat utilization in this study is in sharp contrast to the findings of Baltz et al. (1982) in which competition for preferred microhabitat between two other morphologically dissimilar fishes, dace and sculpin, was mediated by temperature. However, it is probable that temperature differences are largely responsible for the differences in the relative abundances of suckers and trout among reaches.

While we were making the microhabitat observations, we noticed few interactions between species; however, occasionally larger suckers displaced smaller trout from holding or feeding stations. The trout usually returned quickly to their station after the sucker moved through. In contrast to trout, which

Table 3. Intraspecific values of Schoener's (1970) index of overlap in microhabitat variables among size classes of rainbow trout and sacramento sucker

Microhabitat variable		Rainbow trout		Sacramento sucker	
		Juvenile	Adult	Juvenile	Adult
Maximum depth	Y-O-Y	0.65	0.55	0.60	0.68
	Juvenile		0.85		0.85
Focal point depth	Y-O-Y	0.54	0.49	0.96	0.97
	Juvenile		0.87		0.96
Mean water column velocity	Y-O-Y	0.91	0.84	0.71	0.90
	Juvenile		0.94		0.85
Focal point velocity	Y-O-Y	0.85	0.76	0.81	0.80
	Juvenile		0.89		0.94
Surface water velocity	Y-O-Y	0.89	0.83	0.77	0.70
	Juvenile		0.85		0.81
Substrate type	Y-O-Y	0.83	0.79	0.92	0.91
	Juvenile		0.90		0.95

usually hold position in a stream, grazing suckers move about continuously and may displace smaller trout which are near the substrate. Whether or not such displacement constitutes competition depends on its frequency and its significance to the trout in terms of survival, growth and reproduction. We suspect a minimal negative effect since occurrences were rare. The grazing activities of suckers may actually have a positive effect on trout by increasing the availability of drifting prey (Don Erman personal communication). Overall, the few differences found in rainbow trout microhabitat utilization among streams can best be explained by differences in habitat availability rather than competition from suckers. The microhabitat specialization of trout and suckers, like the ecological segregation of size classes within both species, indicates that competition between the species has been minimized by a long history of coevolution (Connell 1980).

The demonstration of direct competition between rainbow trout and Sacramento suckers requires evidence that utilization of a limited resource by one species negatively affects the other species either through interference or exploitation. Despite

many statistical differences in microhabitat utilization, which are based on comparisons of means, our data indicated high interspecific overlap in resource utilization among size classes for most microhabitat variables. However, the low overlap between species in focal point depth and the significant differences between focal point velocities showed that trout and suckers partition the environment vertically. Trout tended to hold position in the water column, while suckers roamed over the bottom, usually remaining in direct contact with it. The greatest overlap between the species occurred between trout alevins and all size classes of sucker. Comparison of Tables 2 and 3 indicates that trout alevins microhabitat utilization generally overlapped as much or more with suckers as with other size classes of trout. Therefore, if interference competition for space is occurring between species the size class most likely affected is trout alevins. Critical experiments to examine the effects of sucker and trout interactions on the growth of trout alevins are needed to test this hypothesis.

Acknowledgements

We thank Robert Burhans, Guy Drapeau, Richard Rieber and Dennis Smith for assistance with the field work, and Jack Holmes and Michael Miller for assistance with the statistical analysis. We also thank Jody Hoffman for recommending the stream system as suitable for our study. This research was supported by the University of California, Water Resources Center, as part of project UCAL-WRC-W-573, and the City and County of San Francisco (Hetch Hetchy Water and Power). Critical reviews by Larry Brown, Don Erman, Bret Harvey, Ned Knight and Bruce Vondracek improved the manuscript.

References cited

- Ashley, P. 1974. The summer feeding ecology of the Humboldt sucker, *Catostomus humboldtianus* and juvenile steelhead *Salmo gairdneri gairdneri* in the upper Eel River System. M.S. Thesis. Humboldt State University, Arcata. 76 pp.
- Baltz, D.M., P.B. Moyle & N.J. Knight. 1982. Competitive interactions between benthic stream fishes, riffle sculpin (*Cottus gulosus*) and speckled dace (*Rhinichthys osculus*). Can. J. Fish. and Aquatic Sci. 39: 1502-1511.
- Bovee, K.D. & T. Cochnauer. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: fishes. Instream Flow Paper No. 3. FWS/OBS-78/33. 39 pp.
- Bovee, K.D. & R.T. Milhous. 1978. Hydraulic simulation in instream flow studies: theory and technique. Instream Flow Paper No. 5, FWS/OBS-78/33. 131 pp.
- Brown, L. & P.B. Moyle. 1981. Impact of squawfish (*Ptychocheilus* spp.) on salmonid populations: a review. N. Amer. J. Fish. Mgmt. 1: 104-111.
- Bryce, G.R. 1980. Data analysis in Rummage - A user's guide. Statistics Department, Brigham Young University, Utah. 172 pp.
- Burns, J.W. 1966. Western sucker. pp. 516-517. In: A. Calhoun (ed.) Inland Fisheries Management, Calif. Dept. Fish Game, Sacramento.
- Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35: 131-138.
- Eschmeyer, P.H. (ed.). 1975. Rehabilitation of fish populations with toxicants: a symposium. N. Central Div., Amer. Fish Soc. Spec. Publ. 4. 74 pp.
- Grossmann, G.D., P.B. Moyle & J.O. Whitaker, Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. Amer. Nat. 120: 423-454.
- Holey, M., B. Holender, M. Imhof, R. Jesien, R. Konopacky, M. Toney & D. Coble. 1979. Never give a sucker an even break. Fisheries 4: 2-6.
- Li, H.W. & P.B. Moyle. 1976. Feeding ecology of the Pit sculpin, *Cottus pitensis*, in Ash Creek, California. Bull. S. Calif. Acad. Sci. 75: 111-118.
- Marrin, D.L. & D.C. Erman. 1982. Evidence against competition between trout and nongamefish in Stampede Reservoir, California. N. Amer. J. Fish. Mgmt. 2: 262-269.
- Moyle, P.B. 1976. Inland fishes of California. Univ. Calif. Press, Berkeley. 405 pp.
- Moyle, P.B. 1977. In defense of sculpins. Fisheries 2: 20-23.
- Moyle, P.B., B. Vondracek & G.D. Grossman. 1983. Response of the fish populations of the North Fork of the Feather River, California, to treatments with fish toxicants. N. Amer. J. Fish. Mgmt. (in press).
- Schoener, T.W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408-418.
- Smith, J.J. & H.W. Li. 1983. Energetic factors influencing foraging tactics of juvenile steelhead trout, *Salmo gairdneri*. Developments in Environmental Biology of Fishes 2: 173-180.
- Snider, W.M. & A. Linden. 1981. Trout growth in California streams. Calif. Dept. Fish and Game, Inland Fish Adm. Rpt. 81: 1-11.