

Habitat Separation of Prickly Sculpin, *Cottus asper*, and Coastrange Sculpin, *Cottus aleuticus*, in the Mainstem Smith River, Northwestern California

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Sympatric coastrange sculpin, *Cottus aleuticus*, and prickly sculpin, *C. asper*, occupied distinct habitats in the mainstem Smith River, northwestern California. For example, 90% of coastrange sculpin (n = 294) used habitat with water velocity > 5 cm s⁻¹, whereas 89% of prickly sculpin (n = 981) used habitat with water velocity ≤ 5 cm s⁻¹. Sixty-five percent of coastrange sculpin were found at depths < 1 m, whereas 37% of prickly sculpin occupied depths > 7 m. The strong spatial separation of coastrange and prickly sculpin in the mainstem Smith River contrasts with the overlap in their use of habitat in the nearby Eel River. Differences between the rivers in habitat availability, intensity of piscivory, and density of sculpins may contribute to this contrast.

PRICKLY sculpin, *Cottus asper*, and coastrange sculpin, *C. aleuticus*, are two morphologically similar benthic fishes that are often sympatric in coastal streams and rivers from Alaska to southern California (Lee et al., 1980). Prickly and coastrange sculpin can be somewhat segregated at the mesohabitat scale in small coastal streams, with prickly sculpin typically occupying pools and coastrange sculpin more often found in riffles (Mason and Machidori, 1976). However, Brown et al. (1995) found no mesohabitat level separation of the two species in the Eel River drainage in northwestern California. Studies of habitat use by prickly and coastrange sculpin have so far not included microhabitat information. These studies have also been limited to depths accessible to backpack electrofishers or seines.

Mainstem river habitat may be important to sculpin populations. Growth rate and size-specific fecundity are positively related to stream size for some populations of mottled sculpin, *C. bairdi*, and slimy sculpin, *C. cognatus*, in the midwest (Anderson, 1985). Coastal populations of prickly and coastrange sculpin are generally assumed to be estuary-dependent for part of their early life history (Mason and Machidori, 1976), with upriver populations maintained by immigration from the lower reaches. In the Eel River drainage, size distributions suggest coastrange sculpin populations are estuary-dependent, whereas prickly sculpin are not, in that young-of-the-year prickly sculpin have been collected over 100 km from the estuary (Brown et al., 1995). At a minimum, mainstem river habitat provides an important migration corridor for both species. To explore the significance of large river habitat to prickly and coastrange

sculpin, we quantified and contrasted their distributions with respect to depth, water velocity, and substrata in the lower Smith River and compared habitat use to habitat availability.

MATERIALS AND METHODS

We conducted field sampling in the Smith River in Del Norte County, California, 8.5-15.8 km upstream from the estuary. The Smith River is the northernmost large coastal river in California, flowing undammed through a 1950 km² drainage basin. Annual precipitation exceeds 200 cm, most of which falls as rain between November and March. Mean discharge for October 1994 through September 1995 3 km upstream from the study reach was 132 m³ s⁻¹. In the winter before this study; flow reached 2300 m³ s⁻¹, an event with a 1.6 y recurrence interval. During the study period, 5-29 September 1995, daily mean discharge averaged 9.1 m³ s⁻¹ (SE 0.27), water temperature ranged 18.2-20.5 C, and underwater visibility was 6-10 m.

The study reach contains deep pools, often with depths > 10 m, alternating with riffles and runs. The substratum is predominantly cobble and gravel. Surrounding vegetation is coastal redwood, *Sequoia sempervirens*, and Douglas fir, *Pseudotsuga menziesii*, with extensive logged areas dominated by brush (e.g., blueblossom, *Ceanothus thyrsiflorus*, and coyote brush, *Baccharis pilularis*).

Native fishes of the Smith River include prickly sculpin, coastrange sculpin, Klamath small-scale sucker, *Catostomus rimiculus*, threespine stickleback, *Gasterosteus aculeatus*, coastal cutthroat trout, *Oncorhynchus clarki clarki*, chinook salmon, *O. tshawytscha*, coho salmon, *O. kisutch*, and steelhead, *O. mykiss*. Pacific lamprey, *Lam-*

TABLE 1. PHYSICAL CHARACTERISTICS OF STUDY SITES IN THE LOWER SMITH RIVER, CALIFORNIA, SEPTEMBER 1995.

	Site 1	Site 2	Site 3
Distance from estuary (km)	8.2	11.2	14.8
Length (m)	310	312	264
Average width (m)	46	49	52
Average depth (m)	1.8	3.3	2.2
Maximum depth (m)	5.8	13.4	8.8
% riffle or run	17	28	24

petra tridentata, occur throughout the basin. Chum salmon, *O. keta*, sockeye salmon, *O. nerka*, green sturgeon, *Acipenser medirostris*, and American shad, *Alosa sapidissima*, are observed rarely.

Confined, high-gradient, bedrock gorges about 6 km upstream of the study reach form partial barriers to upstream migration of sculpin, as indicated by patterns of drift by larval sculpin and the rarity of adults above the gorges (JLW unpubl. data). In contrast, both species of sculpin are common downstream of the gorges. Sculpin density reached 19 fish m⁻² in some areas of the study reach (JLW, unpubl. data).

We collected microhabitat and habitat availability data between 1000 and 1700 h at three sites, each consisting of a pool and adjacent fast water. The sites were chosen to cover the range of habitats available to sculpin in the study section with particular attention to maximum pool depth (Table 1). We made fish observations using SCUBA (or by snorkeling in shallow sections), working upstream and zig-zagging to cover the entire width of the river. Two divers using this procedure covered about 5% of the total area of a site in a single dive. Substrata large enough to conceal sculpin were overturned to expose hidden fish. We recorded data on fish that appeared undisturbed and did not swim away, allowing us to confidently identify species and measure total length (TL) to the nearest 5 mm with a small ruler held within 5 cm of the fish. We estimate less than 10% of the fish encountered fled, with no apparent differences between species or age groups. Fleeing sculpin rarely moved more than a few meters. Zig-zags turned at approximately 60° angles across an average channel width of 49 m (Table 1), spacing which made repeated observations of the same fish on a single dive unlikely. Given the large size of the sites, the large numbers of sculpin, and the fact divers made observations along different pathways on different days, we assumed the likelihood of repeatedly observing the same fish on different days was also negligible. In addition to recording species and TL, we read

depth from a dive gauge (or meter stick in shallow sections), categorized the dominant substratum in 1 m² surrounding the fish [algae, fines (< 4 mm), gravel (4-60 mm), cobble (61-300 mm), boulder (> 300 mm) or bedrock] and characterized water velocity 5-10 cm above the substratum as fast (> 5 cm s⁻¹) or slow (≤ 5 cm s⁻¹). We determined the velocity category by timing particles in the water column passing by a hand-held ruler. Each site was revisited three times at 1-13 day intervals. Habitat availability data were collected separately over nine days following completion of the fish observations. At each site, we laid out cross-stream transects spaced 12 m apart, with the first positioned randomly between 0 and 12 m from the downstream end of the site. We then collected depth, substratum, and velocity information at points every 3 m along each transect, with the first point selected at random 1, 2, or 3 m from water's edge.

For analysis, we separated each species into two age classes, young-of-the-year and adult, based on length-frequency distributions. Log-linear models were used to compare three-dimensional contingency tables (velocity X depth X substratum) among species/age classes and availability (CATMOD Procedure, SAS, vers. 6.11). Substratum data were categorized as either providing cover for sculpin (algae, cobble, boulder) or not (fines, gravel, bedrock). Depth data were condensed into two categories: shallow (:5 1 m), which included most riffle and edge habitat, and deep (> 1 m). To improve performance of the log-linear models, we added 0.5 to the observed cell frequencies (Frigleton, 1984). Because the categorical approach sacrificed considerable depth information, we also compared depths among species/age classes and availability by one-way ANOVA. Pairwise comparisons among species/age classes and availability were made using Dunn-Sidak tests.

RESULTS

We made 1275 observations of fish (981 prickly sculpin, 294 coastrange sculpin) and collected availability data at 1233 points. Young-of-the-year prickly sculpin reached 55 mm and young-of-the-year coastrange sculpin reached 50 mm. Log-linear models comparing young-of-the-year and adults within each species indicated no differences in habitat use (all $P > 0.05$), so we did not separate age classes in subsequent categorical analyses.

Log-linear models revealed distinct differences in habitat use between the two species (Table 2). Coastrange sculpin occupied shallower and

TABLE 2. P-VALUES FOR LOG-LINEAR MODELS COMPARING MICROHABITATS OCCUPIED BY PRICKLY SCULPIN AND COASTRANGE SCULPIN AND AVAILABILITY OF HABITAT IN THE SMITH RIVER, SEPTEMBER 1995.

Source	<i>C. asper</i> vs <i>C. aleuticus</i>	<i>C. aleuticus</i> vs availability	<i>C. asper</i> vs availability
Velocity X Depth X Cover	0.180	0.550	<0.001
Velocity X Depth	0.847	0.164	0.004
Cover X Depth	0.329	0.751	0.180
Cover X Velocity	0.008	0.793	<0.001
Depth	0.023	0.828	<0.001
Velocity	<0.001	<0.001	0.844
Cover	0.236	<0.001	<0.001

faster microhabitats than prickly sculpin (Figs. 1-2). The significant cover X velocity interaction ($P = 0.008$) may be explained in part by the fact that prickly sculpin utilized slow microhabitats without cover to a significant extent (Fig. 2), whereas coastrange sculpin almost never occurred in the absence of cover (12 observations).

Habitat selection was evident for both species when fish distributions were compared with habitat availability (Figs. 1-2). Relative to available habitat, coastrange sculpin selected fast microhabitats and microhabitats with cover (Table 2, Fig. 1). Prickly sculpin strongly selected deep, slow microhabitats with cover (Table 2, Fig. 2).

In contrast to the log-linear model, which used only two depth categories, one-way ANO-

VA of depth data showed that adult prickly sculpin (mean depth = 6.6 m, SE = 0.16, n = 612) occupied deeper habitats than young-of-the-year prickly sculpin (mean depth = 2.9 m, SE = 0.13, n = 369) and coastrange sculpin. Adult coastrange sculpin (mean depth = 1.2 m, SE = 0.10, n = 165) and young-of-the-year coastrange sculpin (mean depth = 1.1 m, SE = 0.10, n = 129) occupied habitats with similar depths. Coastrange sculpin occupied relatively shallow habitats compared to those available (mean depth = 2.4 m, SE = 0.07, n = 1233), and adult prickly sculpin strongly selected deep habitats.

DISCUSSION

Coastrange sculpin and prickly sculpin in the lower Smith River are separated by differences in the depth and water velocity of their microhabitats. High concentrations of adult prickly sculpin at depths > 7 m contributed significantly to this result. One similarity between the two species was a higher use of substrata with cover in shallow water. Increased use of cover in shallow water has been noted for reticulate sculpin, *C. perplexus*, in Oregon (Finger, 1982) and may be a response to a relatively high risk of predation (Harvey and Stewart, 1991).

The pronounced physical separation of sculpins in the Smith River could be generated by ongoing biotic interactions. Interactive segregation among benthic fishes has been observed in previous studies (Finger, 1982; Taylor, 1996). The scarcity of small sculpins in deep habitat in

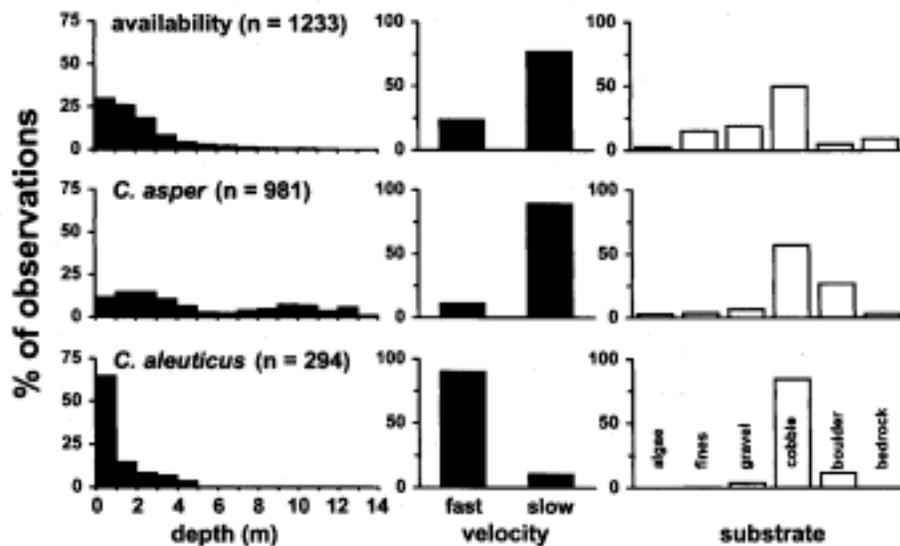


Fig. 1. Univariate display of use of habitat by prickly and coastrange sculpin and habitat availability in the Smith River, September 1995. For velocity: "slow" $\leq 5 \text{ cm s}^{-1}$; "fast" $> 5 \text{ cm s}^{-1}$

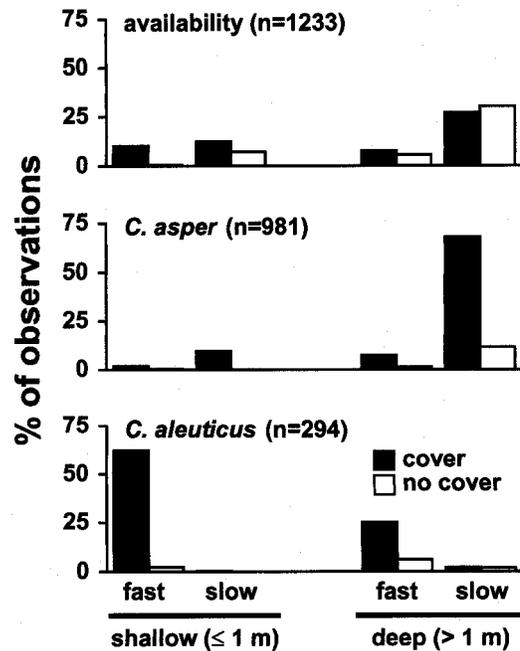


Fig. 2. Categorical display of use of habitat by prickly and coastrange sculpin and habitat availability in the Smith River, September 1995. For velocity: "slow" ≤ 5 cm s^{-1} ; "fast" > 5 cm s^{-1} . For depth: "shallow" ≤ 1 m, "deep" > 1 m. "Cover" includes habitats with algae, cobble, or boulder substrata. "No cover" includes habitats with fines, gravel, or bedrock substrata.

the Smith River could be a response to the threat of predation from large prickly sculpin. Several large prickly sculpin (TL > 150 mm) collected in the study reach contained smaller sculpin (JLW, unpubl. data).

Alternatively, inherent differences in habitat preferences among sculpins (e.g., Brown, 1991) may lead to separation independent of interspecific interactions. For prickly and coastrange sculpins, any innate interspecific differences in habitat preferences could be caused by differences in morphology. Like other benthic fishes (Webb, 1989; Kessler and Thorp, 1993), both species use their pectoral fins to wedge between or cling to the substratum in fast water (JLW, pers. obs.). The ratio of pectoral fin length to standard length for Smith River coastrange sculpin is significantly greater (t-test; $df = 38$; $P < 0.001$) than for prickly sculpin. If longer pectoral fins increase the ability to "grasp" substrata, coastrange sculpin may be better able to maintain position in fast water than would prickly sculpin.

In contrast to the Eel River, where the two species occur at comparable densities in riffle

habitat (Brown et al., 1995), separation of prickly and coastrange sculpin in the Smith River was evident at the mesohabitat scale. Coastrange sculpin comprised 98% of the sculpins we observed in riffles and prickly sculpin 89% of the sculpins we observed in pools. Several factors may contribute to the apparent difference in the mesohabitat scale distributions of the two species in the Eel and Smith rivers. First, piscivorous Sacramento squawfish, *Ptychocheilus grandis*, may affect the distribution of sculpins in the Eel River. Juvenile steelhead and Sacramento suckers, *Catostomus occidentalis*, in the Eel River respond to the presence of squawfish by increasing their use of riffles (Brown and Moyle, 1991). Prickly sculpin in the Eel River may respond similarly, whereas sculpin in the Smith River are relatively free from predation by fish. Second, to the extent both species require unembedded cobbles and boulders, the lack of such habitat in pools of the Eel River (JLW unpubl. data) may force greater overlap of the two species. Third, the relatively low sculpin densities in the Eel River (< 1 fish m^{-2}) may preclude strong interspecific interactions (Brown et al., 1995). These factors are probably not independent. For example, absence of unembedded substrata in pools may exacerbate the effect of Sacramento squawfish on sculpin distributions in the Eel River.

This study shows that coastrange and prickly sculpin populations in the lower Smith River, in contrast to some nearby rivers and streams, occupy distinctly different habitats. The observed habitat separation appears to depend on microhabitat that is frequently unavailable in smaller streams or in large rivers with aggraded channels. The availability of large, unembedded substrata over a broad range of depths in the Smith River may be critical to maintaining its comparatively large sculpin populations. These populations may be of regional importance, particularly if they serve as source populations for surrounding drainages.

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