

## APPLIED ISSUES

# Effects of an introduced piscivorous fish on native benthic fishes in a coastal river

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### SUMMARY

1. We used field surveys to compare the density and mesohabitat-scale distribution of the native coastrange sculpin (*Cottus aleuticus*) and the prickly sculpin (*C. asper*) in coastal rivers in north-western California, U.S.A., with and without an introduced piscivorous fish, the Sacramento pikeminnow, *Ptychocheilus grandis*. We also measured mortality of tethered prickly sculpin in a field experiment including river, habitat type (pools versus riffles) and cover as factors.
2. Average sculpin density (*C. aleuticus* and *C. asper* combined) in two rivers without pikeminnow was 21 times higher than the average density in two rivers in a drainage with introduced pikeminnow. In riffles, differences in the density of sculpins among rivers could be linked to differences in cover. However, riffles in rivers without pikeminnow had an average sculpin density 77 times higher than rivers with pikeminnow, yet only nine times more cover. In pools, cover availability did not differ among rivers, but the density of sculpins in rivers without pikeminnow was 11 times higher than rivers with pikeminnow.
3. In the field experiment, mortality of tethered sculpin varied substantially among treatments and ANOVA indicated a significant River  $\times$  Habitat  $\times$  Cover interaction ( $P < 0.001$ ). Overall, tethered prickly sculpin suffered 40% mortality over 24 h in rivers with pikeminnow and 2% mortality in rivers without pikeminnow, suggesting that predation is the mechanism by which the pikeminnow affects sculpins.
4. The apparent reduction in sculpin abundance by introduced pikeminnow has probably significantly altered food webs and nutrient transport processes, and increased the probability of extinction of coastrange and prickly sculpins in the Eel River drainage.

*Keywords:* Cottidae, field experiment, introduced species, predation, *Ptychocheilus grandis*

### Introduction

Predation by introduced fishes is often cited as a major factor in the decline of native freshwater fishes. In many cases, the importance of predation is inferred from a decrease in abundance or diversity of native species following an invasion by a piscivore (Zaret & Paine, 1973; Townsend & Crowl, 1991; Ogutu-Ohwayo, 1993). Unfortunately, preinvasion informa-

tion on native species is often scarce and fish introductions typically coincide with anthropogenic habitat alteration (Townsend & Crowl, 1991). Such conditions make it difficult to recognize native populations in decline and isolate the factors causing these declines.

When information about preinvasion abundance is lacking, one approach to assessing the impact of fish introductions is to compare otherwise similar systems with and without the introduced species. If differences among the populations of native species cannot be attributed to physical conditions or other biotic interactions, the introduced species is implicated as a

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contributing factor. Experiments may then permit examination of specific interactions between introduced and native species (e.g. Meffe, 1985). We used this approach to investigate the effects of the introduced Sacramento pikeminnow, *Ptychocheilus grandis* (Ayres), on the native coastrange sculpin, *Cottus aleoticus* Gilbert, and prickly sculpin, *C. asper* Richardson, in the Eel River in north-western California, U.S.A.

The Sacramento pikeminnow is a large [commonly > 350 mm standard length (SL)] cyprinid native to the Sacramento-San Joaquin Drainage in the Central Valley of California and several coastal rivers south of the Eel Drainage (Moyle, 1976). Fish are the most common prey of pikeminnow > 250 mm SL (Brown, 1990; Brown & Moyle, 1997; R.J. Nakamoto & B.C. Harvey, unpublished). Illegally introduced into a reservoir in the upper Eel River drainage around 1979, the pikeminnow spread rapidly throughout much of the Eel River (Brown & Moyle, 1997), and now comprises the majority of fish biomass in most large channels in the basin (B.C. Harvey, unpublished).

Coastrange sculpin and prickly sculpin are two small (usually < 130 mm SL) benthic fishes native to coastal streams and rivers in western North America from southern California to Alaska (Lee *et al.*, 1980). The Smith River in north-western California contains coastrange and prickly sculpins at densities up to 19 fish m<sup>-2</sup> (J.L. White & B.C. Harvey, unpublished). In the Smith River, the two species occupy distinct habitats, with coastrange sculpin occurring almost exclusively in riffles and prickly sculpin in pools (White & Harvey, 1999). In contrast, both species are found at similar, low (< 0.1 m<sup>-2</sup>) densities in riffles and runs of the Eel River (Brown, Matern & Moyle, 1995). However, previous research in the Eel River has not included sampling of deep pools.

Differences between these rivers in the densities and mesohabitat-scale distributions of sculpins could be the result of predation by pikeminnow. Where the distributions of pikeminnow and sculpins overlap in the Eel River, the latter comprise 14% by mass of the fishes consumed annually by large pikeminnow (R.J. Nakamoto & B.C. Harvey, unpublished). To investigate further the possible effects of introduced pikeminnow on native sculpin populations, we recorded densities and distributions of coastrange sculpin and prickly sculpin in the mainstem and the South Fork of the Eel River (MS Eel and SF Eel, respectively), and in two rivers without pikeminnow in north-western California. We also quantified habitat availability to determine if differences in the densities or distributions of sculpins could be explained by differences in habitat. Finally, we performed a field experiment to determine if predation by pikeminnow is a probable cause of the differences among sculpin populations.

## Methods

### Study areas

Our study sites were in the lower reaches of the Smith, Mad, MS Eel and SF Eel rivers in north-western California, U.S.A. (latitude 40°–41°50'N, longitude 123°50'–124°10'W). We focused on the lower reaches because mainstem rivers often contain the bulk of prickly and coastrange sculpin populations in coastal rivers (J.L. White & B.C. Harvey, unpublished). Large, deep pools characterize these reaches (Table 1), all of which are bordered primarily by coniferous forest and pastureland.

Climate in the region is marked by wet winters (rainfall > 90 cm year<sup>-1</sup>) and dry summers. Discharge

**Table 1** Physical characteristics of study reaches and study sites

River	Catchment area (km <sup>2</sup> )	Study reach (km from estuary)	Discharge (m <sup>3</sup> s <sup>-1</sup> )		Study site dimensions (m)			
			Mean (range)		Mean (SE)			
			Nov 97 until Mar 98	Jul 98 until Sep 98	Pools (n = 3)		Riffles (n = 3)	
					Length	Width	Length	Width
Smith	1950	10–18	282(5–3562)	11(6–21)	97(8)	57(8)	69(27)	12(21)
Mad	1241	10–17	103(1–505)	< 2(1–3)	111(57)	21(6)	67(15)	10(2)
MS Eel	7969	13–53	516(6–2840)	6(2–15)	204(28)	73(2)	64(30)	46(5)
SF Eel	1764	55–75	111(6–1035)	< 2(1–4)	147(29)	37(2)	61(32)	21(9)

in all four rivers is strongly linked to rainfall, and is moderate to high through the winter and low in the summer (Table 1). Water temperature is typically 6–10 °C in winter and 18–27 °C in summer.

Historically, similar fish assemblages probably occupied the four rivers, comprised largely of anadromous salmonids [chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), coho salmon, *O. kisutch* (Walbaum), and steelhead, *O. mykiss* (Walbaum)] and few year-round residents [prickly sculpin, coastrange sculpin, suckers (Klamath smallscale sucker, *Catostomus rimiculus* Gilbert and Snyder, in the Smith River; Sacramento sucker, *C. occidentalis* Ayres, in the Mad, MS Eel and SF Eel rivers)], threespine stickleback, *Gasterosteus aculeatus* L., resident rainbow trout, *O. mykiss*, and coastal cutthroat trout, *O. clarki clarki* (Richardson). Pacific lamprey, *Lampetra tridentata* (Gairdner), were probably common in all four rivers.

Whereas the fish assemblage in the Smith River is composed almost entirely of native species (J.L. White & B.C. Harvey, unpublished data), numerous species have been introduced into the Mad and Eel rivers. The Mad River contains low numbers of a variety of introduced fishes, including green sunfish, *Lepomis cyanellus* Rafinesque, largemouth bass, *Micropterus salmoides* (Lacepède), and brown bullhead, *Ameiurus nebulosus* (Lesueur) (T.D. Roelofs, unpublished data). None of these species is well adapted to the sustained, high winter flows in north-coastal California streams, so the low densities of these fishes found in the Mad River are probably maintained by immigration from Ruth Lake, an upstream reservoir. Like the Mad River, the Eel River supports low numbers of non-native species adapted to lentic habitats (e.g. green sunfish and brown bullhead), probably washed in from an upstream reservoir (Brown & Moyle, 1997). However, the most abundant introduced fishes in the Eel River system are pikeminnow and California roach, *Hesperoleucus symmetricus* (Baird & Girard) (B.C. Harvey, unpublished data), another cyprinid native to the Sacramento-San Joaquin Drainage and several coastal rivers south of the Eel Drainage (Moyle, 1976).

### Field surveys

After completing a habitat census of each study reach, we randomly selected three pools and three riffles within each reach as study sites. Field crews measured sculpin densities and habitat availability at the

24 study sites from 28 July to 8 September 1998. Observations were made on five to 10 cross-stream transects positioned at randomly selected distances (but at least 3 m apart) along the length of each site. Random numbers were generated using a pocket calculator. In pools, a pair of SCUBA divers worked in single file from bank to bank along each transect, the first diver making fish observations and stringing a measuring tape along the bottom. Following about 4 m behind the first, the second diver collected habitat availability data. In riffles, a snorkeller made fish observations while a second worker followed on foot collecting habitat availability data.

Along each transect, the first person looked for fish in a strip 0.75 m wide on substrata known, based on prior work in one of the study rivers (White & Harvey, 1999), to provide cover for coastrange and prickly sculpin ( $\geq 20\%$  cobbles or boulders with average embeddedness  $\leq 10\%$ ), and in a strip 1 m wide on substrata that did not provide cover. A narrower strip was surveyed on substrata with cover because of the time required to carefully overturn cobbles and small boulders that potentially concealed sculpins. The first person kept a tally of sculpins by species for the 'Cover' and 'No Cover' substratum categories and recorded the total distance along the transect falling into each cover category.

We collected habitat availability data at points spaced evenly along each transect. The spacing of points (X) was selected to yield at least 100 points at each site. The first point on each transect was randomly positioned between 0 and X m from the water's edge. At each point, we read depth from a dive gauge (or metre stick in shallow areas), recorded the percentage of each substratum type in 1 m<sup>2</sup> surrounding the point [fines (maximum diameter < 4 mm), gravel (4–60 mm), cobble (61–300 mm), boulder (> 300 mm) or bedrock], and visually estimated the average embeddedness of cobbles and boulders to the nearest 10%. In riffles, we also measured mean water column velocity at each point with a velocity metre.

We calculated sculpin densities for the two substratum categories within each site by summing the transect data. The  $\log_{10}(x + 1)$ -transformed density data were then checked for homogeneity of variances using the  $F_{\max}$ -test (Sokal & Rohlf, 1995). We compared these densities using three-way analysis of variance (ANOVA) with river, habitat type and cover as factors.

Habitat availability was also calculated by summing the transect data for each site. For the riffle velocity and the pool and riffle depth data, we again checked for homogeneity of variances using the  $F_{\max}$ -test and then compared rivers using one-way ANOVA. Recognizing the strong association of sculpins with cover, we reduced the substratum data to an estimate of the percentage of area in each site that provided cover for sculpins using the equation:

$$\text{Area providing cover (\%)} = A + 0.64B,$$

where  $A$  = percentage of the substratum made up of cobbles or boulders with 0% embeddedness and  $B$  = percentage of the substratum that is made up of cobbles or boulders with 10% embeddedness. The 0.64 multiplier is the proportion of the two-dimensional projection of a sphere that remains after subtracting the area of a 10% embedded portion. The percentage cover values were arcsine transformed and then checked for homogeneity of variances using the  $F_{\max}$ -test. We compared percentage cover among the rivers using one-way ANOVA, testing pools and riffles separately.

### Field experiment

To contrast habitat-specific predation risk among rivers, we measured mortality of tethered prickly sculpin. We employed a three-factor, repeated measures design in which river (Smith, Mad, MS Eel, SF Eel), habitat type (pool, riffle) and cover (Cover, No Cover) were considered fixed factors. The repeated measures consisted of a Cover and a No Cover trial at each of the 24 sites used in the field survey. The response variable was percentage mortality of 10 sculpin after 20–24 h. To reduce confounding of time and treatment, we completed only one-third of the trials necessary for each river during a given visit. We randomized the order of visits to the four rivers and the site/cover combinations within visits. The field experiment ran from 10 June to 24 July 1998.

We collected fish within 12 h of each trial with a backpack electrofisher. Sculpin in the experiment were 40–70 mm SL, a size-range comprising the majority of prickly sculpin in both the Smith (J.L. White & B.C. Harvey, unpublished) and Eel rivers (Brown *et al.*, 1995). In the Smith and Mad rivers, we easily obtained enough fish from riffles and runs near the study sites. Low numbers of prickly

sculpin in the MS Eel and SF Eel rivers made collection of adequate numbers difficult, so we also obtained fish from the Van Duzen River, a tributary to the lower MS Eel River. Fish were transported to the study sites in aerated coolers.

We tethered fish to a 0.4-kg weight with a 0.5 m length of fishing line (2.7-kg test monofilament). Tethers were fastened to the sculpin with a small loop through a needle hole in the preopercle and to the weight with a snap-swivel. We anesthetized fish in stream water with dissolved sodium bicarbonate before piercing the preopercle and attaching the line. Each fish was allowed 20–60 min to recover in aerated river water before being placed in the river.

For each trial, fish were placed at 10 randomly selected locations within a site. Each position was determined by first selecting a random distance along the length of a unit. At that longitudinal distance, a cross-channel location was selected at random from the total width. For No Cover trials, tethered fish were left on gravel, sand, or embedded cobble substrata. Fish in Cover trials were left on the same substratum, but were provided with artificial shelters. Five artificial shelters, each a pair of 30 × 18-cm black plastic plates separated by 2-cm spacers, were arranged in a stacked semicircle at the upstream perimeter of the area accessible to the fish (Fig. 1). Stakes held the shelters in position.

Once in place, tethered fish were left undisturbed for 20–24 h. At the end of each trial, we returned to the sites to record mortality and recover equipment. We returned any surviving fish to the area where they were originally captured.

## Results

### Field surveys

Habitat did not differ significantly among the four rivers with the exception of percentage cover in riffles and pool depth (Fig. 2). ANOVA indicated no significant differences in riffle depth and velocity ( $F_{3,8} = 2.54$ ,  $P = 0.13$  for both) and cover in pools ( $F_{3,8} = 0.83$ ,  $P = 0.51$ ). Variances of the transformed percentage cover data for riffles were not homogeneous, violating an assumption of ANOVA. However, for fixed-effects ANOVA with equal sample sizes, the consequence of heterogeneous variances is normally only a slight increase in  $\alpha$  (Glass, Peckham & Sanders,

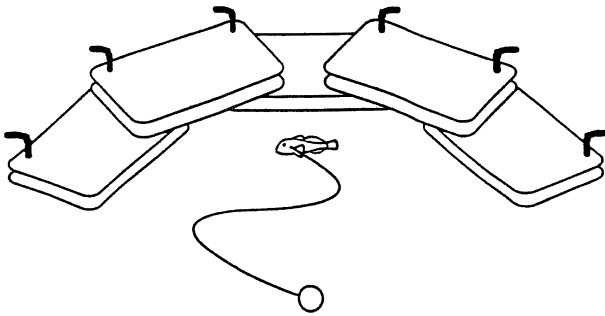


Fig. 1 Arrangement of artificial cover and tethered sculpin in the field experiment.

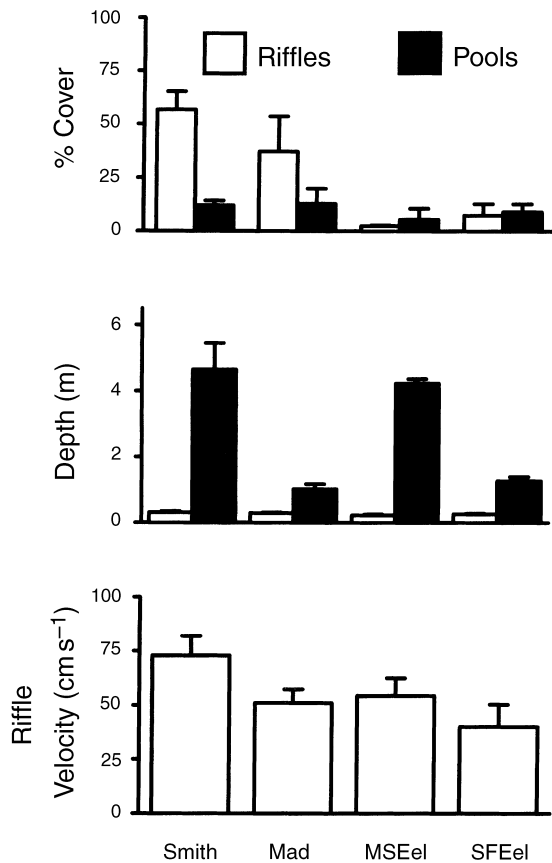


Fig. 2 Habitat availability at the study sites. Percent cover = percentage of total area providing overhead cover. Bars represent mean of three riffles or three pools in each river. Error bars indicate one SE.

1972). Given the strong river effect ( $F_{3,8} = 7.27$ ,  $P = 0.01$ ), a slight increase in  $\alpha$  would not change the conclusion that percentage cover in riffles differed significantly among rivers. Overall, percentage cover in riffles in the rivers without pikeminnow was nine

times higher than in the rivers with pikeminnow. Mean depth of pools differed among rivers ( $F_{3,8} = 20.75$ ,  $P < 0.001$ ), but pairwise comparisons (Dunn-Šidák,  $\alpha = 0.05$ ) grouped the Smith River with the MS Eel River and the Mad River with the SF Eel River. Thus, the pairs of rivers with and without pikeminnow each included one with shallow pools and one with deep pools (Fig. 2).

In the effort to quantify sculpin densities, we examined 5748 m<sup>2</sup> of habitat and observed 1328 sculpins. In all four rivers, sculpins were strongly associated with cover. The density of both species combined on substratum that provided cover averaged 1 m<sup>-2</sup>, over 50 times the average density on substratum without cover. We, therefore, focused our density comparisons on substratum that provided cover.

The ANOVA model indicated highly significant River  $\times$  Habitat interactions for the densities of both species (prickly sculpin  $F_{3,16} = 13.64$ ,  $P < 0.001$ ; coast-range sculpin  $F_{3,16} = 56.26$ ,  $P < 0.001$ ), although variances of the transformed density data were not homogeneous. The River  $\times$  Habitat interactions probably reflect the overall low numbers of sculpin, regardless of habitat, in the MS and SF Eel rivers compared with the high numbers and distinct habitat associations in the Mad and Smith rivers (Fig. 3). Coastrange sculpin were generally more abundant in riffles and prickly sculpin were more abundant in pools (Fig. 3). In riffles, the density of coastrange sculpin differed among rivers, following a pattern that resembled the one for availability of cover. The differences in density, however, were much more extreme than the differences in cover availability. In rivers without pikeminnow, the density of coastrange sculpin in riffles was 77 times higher than the density in rivers with pikeminnow. In pools, the density of prickly sculpin in rivers without pikeminnow was 11 times higher than that in the MS Eel River, and we found no sculpins in pools in the SF Eel River. The strong differences among rivers in sculpin density in pools were not confounded by any significant differences in the availability of cover.

#### Field experiment

In total, we collected mortality data on 468 of the 480 tethered fish in the field experiment. We excluded eight fish from trials in the Mad and Smith rivers

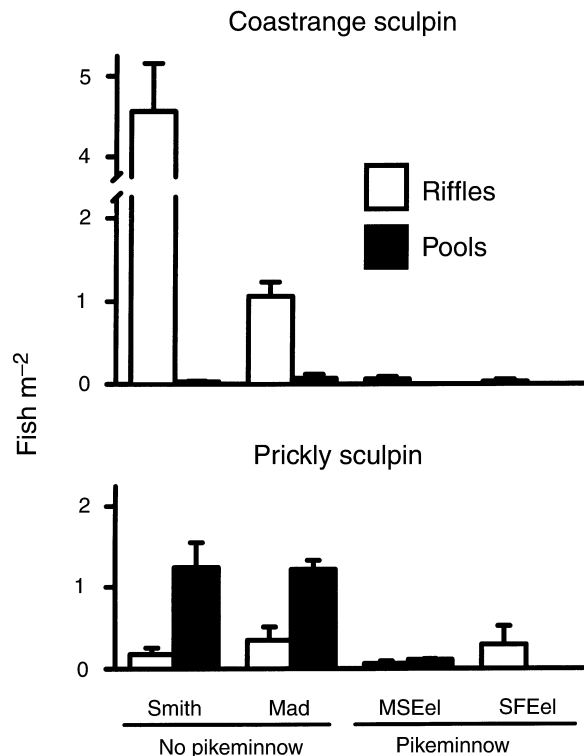


Fig. 3 Density of coastrange and prickly sculpin on substratum with cover (20% cobble or boulder with average embeddedness  $\leq 10\%$ ). Bars represent mean of three riffles or three pools in each river. Error bars indicate one SE.

because their tethers became tangled, confining them beneath artificial shelters, and four fish from trials in the SF Eel River because we could not locate the lead weights (with or without fish) at the end of the trial. On several occasions in the SF and MS Eel rivers, lead weights and intact tethers without sculpin were recovered several metres from their original locations. Upon release, fish either did not struggle against the tether or struggled for a few seconds before settling to the bottom. Fish in Cover treatments moved underneath the artificial shelters shortly after release and moved to different locations beneath the shelters during trials.

The experiment revealed substantial differences in mortality among treatments (Fig. 4). Additionally, mortality did not vary among replicate trials in seven of the 16 treatment combinations. In five of the eight treatment combinations in the Smith and Mad rivers, we observed no mortality in any of the trials (15 trials, 142 tethered fish), while we observed 100% mortality in every trial without cover in pools in the SF Eel River (three trials, 28 tethered fish) (Fig. 4). Although

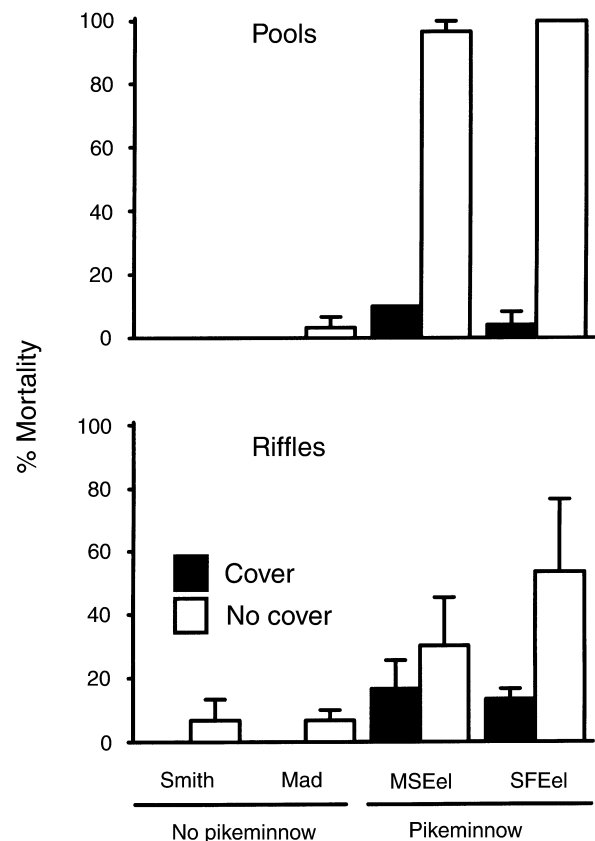


Fig. 4 Mortality of tethered sculpin in 20–24 h trials. Bars represent mean of three trials for each Habitat  $\times$  Cover  $\times$  River combination, 10 fish per trial. Error bars indicate one SE.

variances clearly differed among treatments, we concluded the experiment revealed significant differences based on extremely low  $P$  values (Table 2) and the minimal effect of heterogeneous variances on ANOVA with equal sample sizes (Glass *et al.*, 1972).

All three factors in the experiment interacted to influence sculpin mortality (River  $\times$  Habitat  $\times$  Cover,  $P < 0.001$ ; Fig. 4). In pools, cover substantially influenced mortality in the MS and SF Eel rivers (mean mortality  $> 90\%$  in No Cover trials; mean mortality  $\leq 10\%$  in Cover trials), but had little effect in the Smith and Mad rivers where mortality was universally low. The cover effect was not pronounced in riffles, although treatments with no cover trended toward higher mortality in all four rivers. Overall, tethered sculpin suffered 40% mortality in rivers with pikeminnow and 2% mortality in rivers lacking pikeminnow (where all the sculpin survived in five of the eight treatment combinations). The highest mortality observed in rivers without pikeminnow was

**Table 2** Effects of river, habitat (riffle, pool) and cover on survival of tethered prickly sculpin

Source	d.f.	SSQ	F-value	P-value
River	3	4.7	28.29	< 0.001
Habitat	1	0.3	4.71	0.045
River $\times$ Habitat	3	0.6	3.70	0.034
Site (River $\times$ Habitat)	16	0.9		
Cover	1	2.5	74.27	< 0.001
River $\times$ Cover	3	1.5	15.06	< 0.001
Habitat $\times$ Cover	1	0.6	16.75	< 0.001
River $\times$ Habitat $\times$ Cover	3	1.0	9.46	< 0.001
Cover $\times$ Site (River $\times$ Habitat)	16	0.5		

7% (No Cover trials in riffles in the Smith River). In contrast, in rivers with pikeminnow, mortality exceeded 30% for half of the treatment combinations.

We are confident that the majority of missing sculpin in trials in the MS Eel and SF Eel rivers were consumed by pikeminnow. We observed pikeminnow preying on tethered sculpin on three occasions in the MS Eel River. In all three cases, the tethered sculpin were lying still on the substratum when captured in one strike by a pikeminnow. In one case, a large pikeminnow (> 250 mm SL) consumed a sculpin and dragged the lead weight 5 m from the original position before the tether broke free. We found intact loops at the end of tethers of every missing sculpin, assuring us that sculpin were not working loose on their own, as tethered sculpin could not generate enough force to break through the preopercle. Other potential predators inhabit all four rivers [herons and egrets (Ardeidae), mergansers (*Mergus* spp.), river otters, *Lutra canadensis* (Schreber)] but were rarely seen during the experiment.

## Discussion

This study indicates that introduced pikeminnow have had a severe negative impact on the abundance of sculpins in the Eel River. The pikeminnow has rendered pools in the MS and SF Eel rivers virtually uninhabitable, although pools contain the highest densities of prickly sculpin in nearby rivers without pikeminnow. Additionally, while our study was limited to late summer, pikeminnow predation may have a greater impact on sculpin populations during other times of the year. Both coastrange and prickly sculpin make downstream spawning migrations in the late winter and spring (Moyle, 1976) that involve

moving through pools. While the mortality of free-living sculpins would not be as high as that of tethered sculpins, migrating sculpins moving through pools in the Eel River undoubtedly face a high risk of predation by pikeminnow. Data on the diet of pikeminnow from the Eel River may reflect predation on migrants. Adult sculpins were found in pikeminnow stomachs only during the spawning season for sculpins (February–June), and comprised most of the fish in the pikeminnow diet during that period (R.J. Nakamoto & B.C. Harvey, unpublished data).

Although both sculpin species are exposed to pikeminnow predation during spawning migrations, the coastrange sculpin population in the Eel River may be more strongly affected by pikeminnow predation on juveniles than prickly sculpin. Larvae of both species drift but, unlike prickly sculpin, larvae of coastrange sculpin in the Eel River appear to require estuary habitat for larval and early juvenile development (Brown *et al.*, 1995). This life history necessitates lengthy upstream migrations by young-of-the-year fish. A higher rate of predation on migrating juveniles may explain why we found no 0+ coastrange sculpin in either the MS Eel or SF Eel rivers, whereas nearly 50% of the prickly sculpin were 0+ fish. In contrast, in the rivers without pikeminnow, 0+ fish comprised over 50% of the coastrange sculpin and 18% of the prickly sculpin.

In response to the presence of large, piscivorous fish in pools, some fish shift to riffles (e.g. Schlosser, 1988; Brown & Moyle, 1991). However, several observations in addition to the results from our experiment suggest that a habitat shift to riffles in the Eel River would not alleviate the strong impact of pikeminnow on sculpin abundance. Large (> 350 mm SL), radio-tagged pikeminnow in the SF Eel River move from pools into riffles and runs at night, presumably seeking prey (Harvey & Nakamoto, 1999). Pikeminnow large enough to consume sculpin have also been observed actively foraging in riffles in the MS and SF Eel rivers during the day (J.L. White, unpublished data). Additionally, fish in shallow habitat can be exposed to a greater risk from other predators, such as birds and mammals (Harvey & Stewart, 1991). In rivers without pikeminnow, predation by birds and mammals in shallow water may explain why cover affected mortality in riffles but had little or no effect in pools. Finally, by limiting both sculpins to riffles, pikeminnow not only restrict the amount of living space, but

also prevent the distinct mesohabitat-separation displayed by the two species in rivers without pikeminnow (this study; White & Harvey, 1999).

Physical conditions in the MS Eel and SF Eel rivers may affect sculpins irrespective of the presence of pikeminnow. Clearly, riffles in the MS and SF Eel rivers have substantially less cover than riffles in the Mad and Smith rivers. However, we believe it is unlikely that the differences in cover availability alone can explain the extreme differences in sculpin densities. More likely, physical conditions in the Eel River have exacerbated the effect of pikeminnow on sculpin abundances. Large floods in the mid-1950s and 1960s produced substantial aggradation in rivers throughout north-west California. Channels are now generally wider and shallower than they were prior to the floods; riffles and pools are less distinct, blending into homogeneous runs; and bed material is dominated by small gravel (Lisle, 1982). For sculpins, the critical result of these changes is a reduction in the availability of large, unembedded substratum particles in both pools and riffles. Our field experiment suggests that these conditions increase the risk to sculpins from pikeminnow.

The severe reductions in what were probably two of the most abundant fishes in the MS Eel and SF Eel rivers may have had ecosystem-level consequences. For example, sculpins may play an important role in river food webs as prey. In a study of the winter diet of river otters in Oregon, U.S.A., sculpins were the most frequently encountered food item, occurring in 31% of otter stomachs (Toweill, 1974). Sculpin larvae may also be an important prey. We have recorded as many as 32 sculpin larvae  $m^{-3}$  in the drift just upstream of the Smith River estuary (J.L. White & B.C. Harvey, unpublished). The larvae remain for days to weeks in estuaries (Moyle, 1976), serving as a potential food source for many organisms, including juvenile salmonids (Heard, 1965). In contrast to the Smith River, the highest observed density of sculpin larvae in the lower Eel River was 0.02 fish  $m^{-3}$  (J.L. White & B.C. Harvey, unpublished).

The use of estuaries as rearing habitat by sculpins also raises the possibility that they have an important role in large-scale, upstream transport of nutrients. This process may be a critical component supporting ecosystems in the Pacific Northwest (Gresh, Lichatowich & Schoonmaker, 2000). Historically, large runs of anadromous salmonids represented the overwhelming majority of the upstream transport of nutrients in

coastal streams. At present, with salmon populations low, prickly and coastrange sculpin may have a significant role in this process.

Overall, the introduction of the pikeminnow and California roach into the Eel River has resulted in a fish assemblage similar to those found in parts of the Sacramento-San Joaquin Drainage (Brown & Moyle, 1997). Neither sculpin species native to the Eel River has been extirpated and sculpin distributions at the mesohabitat scale in the Eel River resemble those in streams with native sculpin and pikeminnow populations. For example, in tributaries of the Sacramento River, the riffle sculpin, *C. gulosus* (Girard), occupies riffles and adult pikeminnow are found mostly in pools (Moyle & Baltz, 1985). However, by severely reducing sculpin abundances in the Eel River, introduced pikeminnow undoubtedly have increased the probability of extinction for coastrange and prickly sculpin populations in this system, while also altering the food web and ecosystem processes.

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